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LONDON SCHOOL OF HYGIENE AND TROPICAL MEDICINE.
RESEARCH WORKERS IN HELMINTHOLOGY, DECEMBER, 1926.



D. O. MORGAN. W. McDONALD. T. W. M. CAMERON. J. CARROLL. J. N. OLDHAM. M. A. AZIM. B. G. PETERS.
M. TRIFFITT. T. GOODEY. R. T. LEIFER. R. J. ORTLEPP. J. LEISHMAN.

**Studies on Three New Genera and some Little-Known Species of the Nematode Family
Protostrongylidæ Leiper, 1926.**

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INTRODUCTION.

THE classification of the nematodes occurring in the lungs (and related forms) of land mammals has always been one of considerable difficulty, in large part because of the existing very inadequate descriptions of many of the commoner forms. Most systematic helminthologists have followed and amplified the classification adopted by Railliet and Henry in 1907, a system which divided these nematodes into three main groups—those found in the blood-stream (*Hæmostrongylus*); those found in the larger bronchi (*Dictyocaulus*, *Metastrongylus* and *Crenosoma*); and those found in the minute bronchi and alveoli (*Synthetocaulus*). While the first two groups contain four well-defined zoological species, an examination of the forms included in the genus *Synthetocaulus* shews that it consists of a heterogeneous collection of species, which, although possessing a common habitat, are by no means so closely related as has been supposed, and, indeed, belong to several different genera.

Railliet and Henry defined the genus *Synthetocaulus* as follows:—

Hair-like body. Mouth with three binocular lips. Posterior body of male reinforced by a chitinous arc. Bursa with anterior and median

rays split, posterior reunited in a large trunk with a very thick wall. Two punctate striated or pectinate spicules, gently curved. Between them and the front of the bursa are large thick chitinous teeth forming an open angle behind. There are also two chitinous appendices of unknown significance, of very constant shape and forming with the spicules excellent specific characters.

Vulva a little in front of anus. Uteri convergent. Eggs with no trace of segmentation when deposited. Embryo with a tail prolonged by an undulating appendix.

They designated as type the species *S. commutatus*.

Two years previous to this paper, however, Kamensky had created the genus *Protostrongylus* to contain the species *P. rufescens* (type), *P. terminalis* (= *P. commutatus*) and *P. pusillus* (= *P. abstrusus*). As the species *commutatus* is obviously congeneric with *rufescens*, the genus *Synthetocaulus*, which must therefore be regarded as synonymous with *Protostrongylus*, has accordingly been suppressed by Leiper (1926).

The description of none of the forms included in Railliet and Henry's genus is adequate—in some cases it is very inadequate; and accordingly Professor Leiper suggested that the writer should undertake a revision of their morphology. He placed at my disposal specimens which had been collected over a period of several years, and I have to acknowledge my indebtedness to him, not only for this, but for the very material assistance he has given me during this study.

There has been a great deal of confusion about the specific identity of the species of *Protostrongylus* from herbivores—the species *P. abstrusus* is, as will be shewn later, not congeneric with *P. rufescens*—and as the most important paper since Mueller's revision of the group is that by Kamensky, which does not seem to be generally available, it may be opportune to refer briefly to his main conclusions.

He points out that Mueller, in 1889, regarded *Strongylus rufescens* and *S. commutatus* as identical, but that Railliet regarded them as distinct species. Nicoolin, a pupil of Kamensky's, carried out a series of examinations of the lungworms of hares in Russia and found that two species were present. These Kamensky regards as *P. rufescens* and *P. commutatus*, and he gives the following table of differences between them :—

<i>P. rufescens.</i>	<i>P. commutatus.</i>
Body visibly narrowed towards ends.	Body same width for entire length but slightly narrower at ends.
Mouth with three bifurcating papillæ.	Mouth with three minute papillæ.
Male 13 mm. to 30 mm. long by 0.12 mm. to 0.2 mm. broad.	Male 20 mm. to 40 mm. by 0.12 mm. to 0.18 mm. broad.
Median and postero-external rays long and rise separately.	Rays short, and rise from common trunks.
Posterior ray slender without incisure.	Posterior ray thick with incisure.
Spicules 250μ to 330μ long. Anterior ends thickened and often project outwards near accessory pieces.	Spicules 110μ to 118μ long. Anterior ends frayed, posterior ends often situated far from accessory pieces.
Female 20 mm. to 70 mm. long by 0.16 mm. to 0.2 mm. broad.	Female 77 mm. to 90 mm. by 0.15 mm. to 0.2 mm.
Posterior end with well-developed boss on ventral side.	Slightly developed papilla on ventral side.
Vulva with "provagina."	Vulva without provagina but with slightly projecting edges.
Vagina 530μ to 700μ long.	Vagina $300\mu(?)$ to 700μ long.
Ova 60μ to 85μ by 33μ to 75μ .	Ova 90μ to 120μ by 16μ to 20μ .
Embryo 180μ by 13μ .	Embryo 300μ to 700μ by 16μ to 20μ .

Kamensky believes that the first of these species (*P. rufescens*) identical with Mueller's *Strongylus sagittatus*. He points out that the spicules in these species from hares will look bifurcated, and considers that this appearance in *Strongylus sagittatus* is merely an optical illusion. He believes that Railliet (1895) has confused *sagittatus* and *commutatus* in his description of *rufescens*.

I have been unable to find any trace of the "provagina," however, in the specimens of *Protostrongylus rufescens* found in Britain. It is figured by Mueller for *Strongylus sagittatus* and by Neveu Lemaire for *Synthetocaulus rufescens*. On the other hand, Railliet makes no mention of this structure in his descriptions of the latter species, and his description agrees with the present specimens.

Accordingly it would seem possible that both Kamensky and Lemaire were actually dealing with *Strongylus sagittatus* and not with *S. rufescens*. If this is so, we can recognise at least three well-defined species of *Prostrongylus*, viz., *Prostrongylus sagittatus* (with a vulvar flap) and *P. rufescens* and *P. commutatus* (without vulvar flaps, but with a telemon which is, respectively, serrated or boot-shaped). It is also possible that *P. ocreatus* and *P. unciphorus* are synonymous with *P. commutatus*, but in the absence of material of the two latter species, it is not desirable to make any change in their nomenclature.

PROTOSTRONGYLUS RUFESCENS (Leuckart, 1865) Kamensky 1905.

It is popularly believed that this species is a common parasite of sheep in Britain; the writer's own experience, however, is that it is the least common of the three species occurring in the lungs of sheep in this country.

In addition to its occurrence in the sheep, it has been reported from hares and from rabbits; in the light of recent investigations, however, its presence in these animals will require to be confirmed as it is possible that it is really *Protostrongylus sagittatus* which has been found and mistaken for this species.

The average length of the specimens examined was 26 mm. in the case of the female and 17.5 mm. in the case of the male.

The cuticle appears to be unstriated even when viewed under the oil-immersion objective. There are two minute cervical papillæ present about the level of the middle of the œsophagus. The simple mouth aperture is surrounded by six very low papillæ.

The œsophagus has a length of about 0.25 mm. and a maximum diameter of 0.04 mm. It has a very slight posterior swelling. The excretory pore is situated just in front of this bulb, at the same level as the nerve ring. The cervical glands are very long and conspicuous, about a sixth of the body length.

The male possesses a single typical genital tubule. The bursa (fig. 1) is very small, but is very characteristic and quite unlike any of the other genera of the *Protostrongylidæ*. The body proper is sharply truncated and flat. On the dorso-lateral margins of this surface are two stout curved cuticular plates, of a roughly crescentic outline. These serve

as supports for the bursal membrane, and are probably analogous to the structures seen in *Triodontophorus* and allied genera, but are much more highly developed. Owing to their presence it is impossible to flatten the bursa for study. Their position also gives the bursa a collar shape, with a ventral opening. There is no dorsal lobe present.

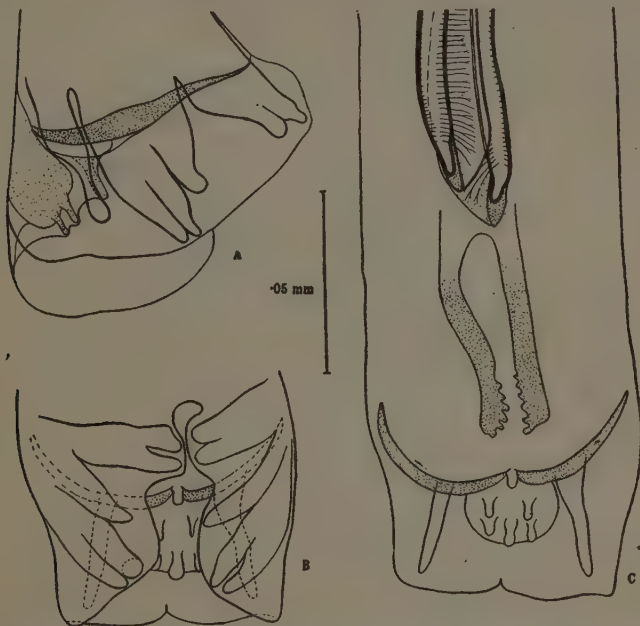


Fig. 1.—*Protostrongylus rufescens*. Bursa of male. A, lateral view. B, ventral view. C, ventral view but with ventral portion removed to shew dorsal rays, telemon and spicules.

All the conventional rays can be identified, but as in the other members of the Protostrongylidæ, they tend to become atypical. The ventral rays are short and stumpy, but extend to the bursal margin. The externo-lateral is shorter than the other lateral rays, all three of which lie close together. The externo-dorsal ray is comparatively slender and ends some distance from the edge of the bursal membrane. The dorsal ray has disappeared as a ray and is replaced by a solid spherical body. On the inner surface of this (fig. 1) are six papillæ arranged in

three groups—three posterior, two median and one anterior—at the junction of the two crescentic cuticular plates referred to above. A reflection of the bursal membrane is carried over these papillæ to form a kind of accessory bursa, of a totally different structure from that seen in the genus *Ostertagia*.

The accessory genital organs in the male consist of two equal and similar spicules, a gubernaculum and a telemon.

Following Railliet (1895), Hall (1916) and Neveu Lemaire (1918) have given the length of the spicules in this species as varying between 110μ and 310μ . In 1907, however, Railliet and Henry gave the length as 240μ to 265μ . It seems probable that the original measurements were due to confusing more than one species under the same name, as such a variation in length—especially as the spicules in the other members of the genus vary only very slightly—is highly improbable.

The spicules are 0.26 mm. in length. Each consists of a central cuticular tube (fig. 1c) and a voluminous spicular sheath. The central tube is of a light brownish colour. Anteriorly it carries a number of irregular projections for the attachment of the very long spicular muscles; posteriorly it ends in a blunt point. This point is surrounded by a colourless cuticle. This tube itself is of a fairly regular diameter, but is curved laterally, so that when the two spicules are partly protruded they have an X appearance. From the ventral aspect of each spicule arises two series of digitations which carry the spicular sheath: the median row of digitations are relatively long, whereas the lateral row is short. These digitations are finely granular, are of irregular shape and often bifurcate. Both series tend to become much smaller in the anterior part of the spicule. The spicular sheath is very large and extends to the entire length of the spicule. It is about twice to three times the diameter of the cuticular tube.

The accessory male organs found in nematodes have long been used as specific characters of some importance, but, while it was recognised that more than one structure in addition to the spicules was involved, it was not until 1921 that a definite terminology was applied to them. Hall then stated: "The gubernaculum and telemon appear to be modifications of the cloacal wall, either by local thickening and condensation of material of suitable hardness for the protection of the cloacal walls

from the passage of the sharp pointed spicules and for the direction of the spicules; they also support the cloacal wall and aperture, the spicules when these are extruded, and the genital cone in some cases; a plate-like gubernaculum projecting from the dorsal wall of the cloaca may also aid in separating the spicules to form a suitable channel for the passage of the spermatozoa. Apparently the term *gubernaculum* should be restricted to the more or less longitudinal structure in the dorsal wall of the cloaca toward the anterior end, and the term *telemon* used for the supporting structure of variable form near the cloacal aperture."

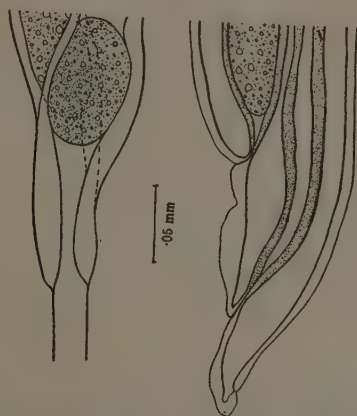


Fig. 2.—*Protostrongylus rufescens*. Left. Commencement of vagina. Right, Vulva and anus.

Hall shews that the term gubernaculum (which means a guiding structure) has in many cases been used for what is functionally a telemon (which means an ornamental supporting structure). Accordingly, in this paper, the term accessory piece or pieces is used in a general sense to include both or either of these structures, and the terms gubernaculum and telemon used in the sense described above.

The accessory pieces are two in number. The gubernaculum is situated about 0.3 mm. from the cloacal opening and consists of a flat arc-shaped plate of a dark brown colour with its concave side on the posterior aspect. Attached to the ventral surface is a central keel

which often bifurcates distally, and on either side of which pass the spicules.

The telemon in this species consists of an H-shaped structure about 0.06 mm. long which is only pigmented in its posterior portion. The non-pigmented portion gradually passes into the substance of the canal wall. The posterior pigmented portion consists of the bottom arms of the H, and therefore appears under the low powers as two separate bodies of a brown colour. It is 0.05 mm. long. On the median aspect of the distal portion of each of these arms appear four or five blunt teeth (fig. 1c).

The female genitalia is double and consists of two ovarian tubules which rise just behind the end of the cervical glands and almost exactly at the same level. They pass together almost without convolutions to the posterior region of the body, where they form the dilated uteri. At about 0.6 mm. from the vulva the uteri unite for form a single long vagina. The anterior portion of this is strongly muscular, but the remainder of the tube is thin-walled and non-muscular and contains the large eggs. This tube opens at a vulva situated at about 0.15 mm. from the tip of the tail. I have been unable to find any trace of a "pro-vagina" or "vulvar flap" mentioned by Kamensky, Neveu Lemaire and other authors.

The female genital tube with its long vagina superficially resembles that seen in *Mecistocirrus*. In that form, however, there is a typical double ovejector, and the vagina is actually the same structure as seen in the other Trichostrongyles, but enormously lengthened. In this case, however, the vagina is equivalent to the true vagina and the ovejectors combined, the first muscular part taking the place of the pars haustrix of both ovejectors in *Mecistocirrus*, the long second, amuscular part, being the pars ejectrix plus the vagina. In other words the apparent similarity between *Mecistocirrus* and *Protostrongylus* is the result of convergence and is only superficial.

The anus is situated about 0.06 mm. from the tip of the tail and the rectum is very short. The tail is short and bluntly pointed (fig. 2). A pair of small caudal papillæ are present, but they do not penetrate the cuticle.

PROTOSTRONGYLUS OCREATUS (Railliet and Henry, 1907).

This species was described by Railliet and Henry in 1907 very briefly as follows :—

“Spicules 290μ to 330μ long, pectinate with bifid tip. Accessory organs, boot-shaped, measuring 70μ to 75μ . From sheep in Algeria.”

Some years ago, Professor R. T. Leiper had collected some specimens of *Protostrongylus* from sheep in Egypt, and these he placed at my disposal. They differ in some respects from Railliet and Henry's description of *P. ocreatus*, especially in the fact that the spicules are not bifid ; but it seems probable that they really belong to this species.

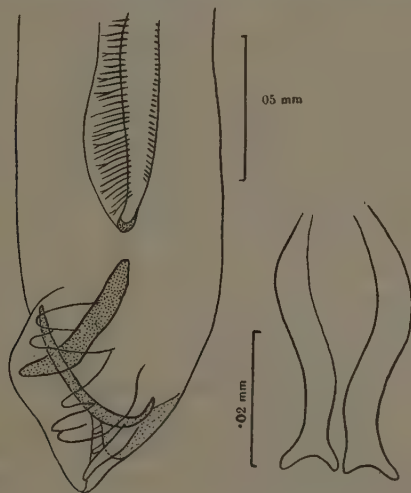


Fig. 3.—*Protostrongylus ocreatus*. Male, shewing bursa and telemon.

When the spicules are retracted, the spicular sheath gives the illusion of a bifid spicule, and it is possible that this appearance misled the original authors. The geographical distribution and the shape of the accessory organs do not differ, and in consequence I tentatively place these specimens in the species *ocreatus*.

The length of the male is about 15 mm. and of the female 24.5 mm. The male closely resembles the type species in size, shape of bursa, spicules and gubernaculum. The spicules measure 0.25 mm. The telemon, however, differs considerably, and resembles, as Railliet and

Henry have stated, a pair of top-boots. The top of this pair of boots is connected, as in *P. rufescens*, by a colourless structure. The pigmented parts are 0.04 mm. long and are split distally. There is no trace of the teeth seen in the type species (fig. 3).

The female closely resembles the type also. There is a slight swelling posterior to the vulva, however, which is not seen in *P. rufescens*. The vulva is 0.15 mm. and the anus 0.06 mm. from the tip of the tail.

PROTOSTRONGYLUS COMMUTATUS (Diesing 1851) Kamensky 1905.

I have been unable to examine any specimens of this species. It is stated to be very common in Central Europe, but I have been unable to find it in England, although, thanks to the courtesy of the Manager of the Game Department of Messrs. Harrods, I have been given the opportunity of examining the lungs of some 100 English hares.

In 1802, Froelich described, under the name of *Filaria pulmonalis*, a nematode parasite from the lung of the hare. Hall (1916) considers that this species was what we now call *commutatus* and has accordingly placed the latter name as a synonym of *pulmonalis*. Kamensky (1905) however, has shewn that both *rufescens* and *commutatus* at least are found in the lung of the hare. It is impossible to say to which of these Froelich's description applies—if either—and in the meantime it seems desirable to neglect his name and use the more familiar *Protostrongylus commutatus*.

The morphology of this form has been investigated by several authors, and an excellent summary of its characters, so far as they are known, has been given by Hall (1916). It does not seem to differ in any essential characters from *P. rufescens*, but until this form has been re-described it seems impossible to delineate its actual differences. Its telemon appears to be identical with that of *P. ocreatus*; indeed it is only on measurements that it can be at present distinguished from that species.

	<i>P. ocreatus.</i>	<i>P. commutatus.</i>
Length of female	24.5 mm.	28-50 mm.
Vulva from tail	0.15 mm.	0.2 mm.
Anus from tail	0.06 mm.	0.1 mm.
Length of male	15 mm.	18-30 mm.
Spicules	0.25 mm.	0.16 to 0.17 mm.
Telemon	0.04 mm.	0.033 mm.

None of these differences seems to be very fundamental, and it is possible that *Protostrongylus ocreatus* should be regarded as a synonym of *P. commutatus*. This cannot definitely be done, however, until the specimens from hares, as well as the type specimens of *P. ocreatus* are examined in the light of modern investigations.

PROTOSTRONGYLUS UNCIPHORUS (Railliet and Henry, 1907).

Material of this form was not available for study, but from the meagre details given by the original authors in their description, it seems probable that it belongs to this genus. It was found in the sheep and goat and is described as follows: "Spicules 250μ to 260μ long, pectinate with extremity rounded and hirsute. Accessory organs recurved in the form of a hook and measuring from one end to the other, 50μ to 60μ ."

It is possible that this is the same species as has been described above as *P. ocreatus*.

PROTOSTRONGYLUS SAGITTATUS (Mueller, 1891).

This species was described from the lungs of *Cervus elaphus*, the only material available being a single male and three to four females. It seems to be closely related to *P. rufescens*, but does not seem to be identical with it. The spicules are described as being bifurcated, although this may be an optical illusion, while the accessory pieces are of different shapes to the type. The cuticular plates in the bursa are not mentioned. Moreover, a vulvar flap is present in the female.

The spicules are said to be about 330μ long and the telemon 33μ long. Kamensky considers that his forms from the hare are identical with this species, and it is possible that this is the form considered by Lemaire to be *S. rufescens*.

SYNTHETOCAULUS LINEARIS Marotel, 1913.

I have been unable to obtain access to the original description of this species by Marotel. Lemaire states of it that the spicules are long, linear and pectinate; moreover they are not equal in length, the larger measuring 320μ to 360μ and the smaller only half this size. There is also present a gubernaculum in the form of a "gouttière entire" which measures 55μ to 70μ long. In front of the bursa are two chitinous arcs, colourless and parallel. The median dorsal ray is very short and comb shaped. The lateral and ventral rays are more divided than

in *commutatus*. Apart from the different size of the two spicules, it would appear to be related to *Protostrongylus*, but as such a character would appear to be fundamental, it is left under its old generic name until its description becomes accessible.

ÆLUROSTRONGYLUS ABSTRUSUS (Railliet, 1898).

Originally described as *Strongylus pusillus* by Mueller, the specific name of this species was altered to *abstrusus* by Railliet as the old name was preoccupied. It has been placed in the genus *Protostrongylus* by Kamensky and in the genus *Synthetocaulus* by Railliet and Henry. It does not, however, belong to the same genus as *P. rufescens*, as is obvious from the following description. Both telemon and cuticular plates are absent and the median dorsal ray is normal in type.

Accordingly the new genus *Ælurostrongylus* is created for its reception.

It was unfortunately not possible to obtain any unbroken specimens of this species, but sufficient fragments and nearly complete forms were recovered from the lungs of cats to enable the size to be stated as approximately 4 mm. in the male and 9 mm. in the female.

The mouth opening is surrounded by six inconspicuous papillæ, and opens directly into the short almost cylindrical œsophagus which is about 0.25 mm. long. The excretory pore and the nerve-ring are in the usual positions.

The male has a small but well-formed bursa present (fig. 4) which is complete and undivided. The ventral rays are blunt and lie close together but are separated by a considerable gap from the lateral group. The lateral rays are also close together, and close to them arises the externo-dorsal ray. The dorsal ray is broad and bifurcates early; and the stout bifurcations give it a Y shape. There are traces of secondary bifurcations in each of the main stems, but none were actually seen in my specimens. In this respect the dorsal ray differs from that drawn by Mueller (1890), where the main bifurcations are separated from their base and the central stem is missing. The cuticular bursal supports seen in *Protostrongylus* are absent.

The spicules are similar and equal, and measure 0.075 mm. in length. Each consists of a cuticular tube, which is swollen anteriorly but terminates in a blunt point. To each is attached a voluminous sheath which is transversely striated but which is without the supporting fingers seen in *Protostrongylus*.

The gubernaculum (fig. 5), which is 0·015 mm. long, has a flat base, from the anterior end of which rises a central structure which carries

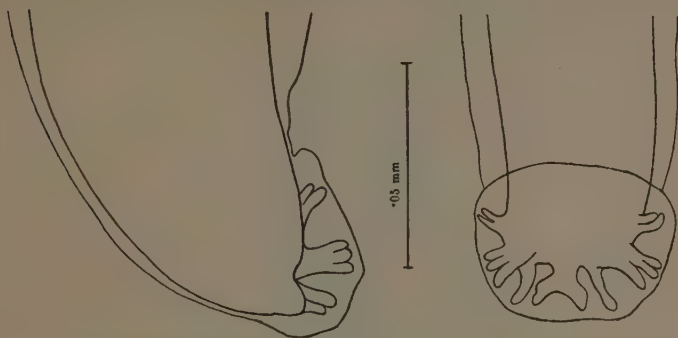


Fig. 4.—*Aelurostrongylus abstrusus*. Male bursa, lateral and ventral aspects.

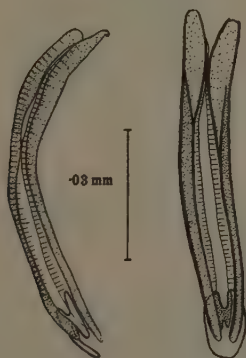


Fig. 5.—*Aelurostrongylus abstrusus*. Spicules and gubernaculum.

anterior and posterior prolongations. The spicules pass on either side of these. There is no telemon present.

The female has a double genital system which is only very slightly convoluted. The tail is bluntly pointed and there are no papillæ present. The anus is 0·04 mm. from the tip of the tail and the rectum is very

short. The vulva is 0.09 mm. from the anus and communicates with a long single vagina, which in turn joins the two parallel uteri. The vagina is about 1.5 mm. long and contains unsegmented eggs measuring about 80μ long by 70μ broad.

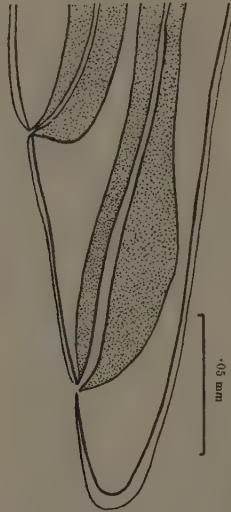


Fig. 6.—*Aelurostrongylus abstrusus*. Tail of female.

MUELLERIUS CAPILLARIS (Mueller, 1889).

By far the commonest nematode parasite of the lungs of sheep is the form first described by Mueller in 1889 under the name of *Pseudalius capillaris* and in 1907 transferred by Railliet and Henry to their new genus *Synthetocaulus*. It is not, however, congeneric with *Protostrongylus rufescens*, neither does it belong to the genus *Pseudalius*. Accordingly, the new generic name *Muellerius* is proposed for it.

The length of the male is about 12 mm. and of the female about 19 mm. The cuticle is very finely striated, but the striations can only be observed under the high powers of the microscope.

The cephalic extremity is very similar to that of *Protostrongylus*.

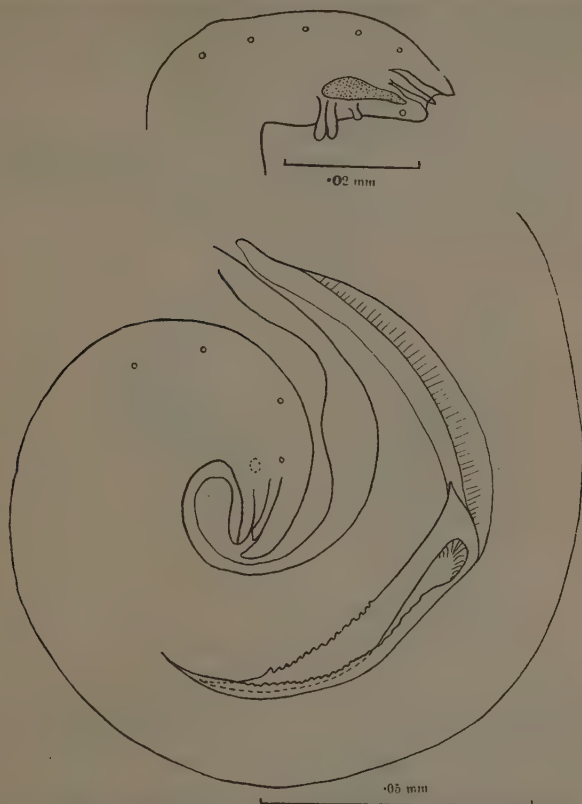


Fig. 7.—*Muellerius capillaris*. Below, tail of male shewing one spicule. Above, cloacal region of male.

The posterior extremity of the male forms a spiral of seven to nine turns similar to that seen in some of the Filarioidea. There is no bursa present, but a number of caudal papillæ are found. Close to the anogenital opening, which is terminal, is a pair of small, sessile papillæ; a short distance in front of this is a pair of small pedunculated papillæ, while just anterior to this are two pairs of rather larger pedunculated papillæ. Neither bursal membrane nor alæ are present.

A small telemon is present. It consists of two conical homogeneous cuticular rods 0.013 mm. long. No gubernaculum can be seen.

There are two equal and similar spicules of a very characteristic shape. Each (only one is shewn in fig. 7) resembles a bent tuning fork and measures 0.15 mm. in length. The handle, which is about half the length of the spicule, is gently curved and carries a voluminous spicular sheath supported by cuticular digitations as in *Protostrongylus*. The blades of the tuning-fork are also curved and are serrated on their concave side. Each blade terminates in a sharp point.

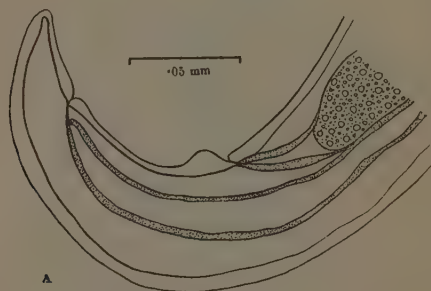


Fig. 8.—*Muellerius capillaris*. Tail of female.

The female has the same general type of genitalia as is found in the other members of this group. The anus is about 0.04 mm. from the tip of the blunt tail (fig. 8) and the vulva is about 0.07 mm. anterior to the anus. There is a slight cuticular swelling just posterior to the vulva.

The vulva is connected by a long tubular vagina, about 0.62 mm. long, to the two uteri. The larger part of this tube is relatively free from muscular fibres, but it is much thicker than is the corresponding part of *P. rufescens*. The anterior portion—about 0.12 mm. long—is surrounded by a stout band of muscular fibres, corresponding in function with the pars haustrix of the *Trichostrongylidæ*.

The egg in the vagina is about 100μ by 20μ broad. From this egg, which is deposited in an unsegmented condition in the alveoli, develops

a larva which closely resembles those of *P. rufescens*. It is 0.25 mm. long and has a posterior undulating appendix. The anus is 0.022 mm. from the tip of this. The length of the cesophagus is 0.075 mm., and it has a double muscular bulb (fig. 9). The posterior portion of the

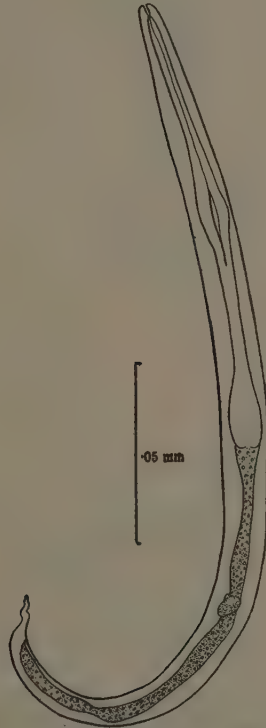


Fig. 9.—*Muellerius capillaris*. Larva.

cesophagus seems to be largely glandular, while the anterior portion is mainly muscular. The genital rudiment lies about the junction of the anterior and middle thirds of the intestine.

PSEUDOSTRONGYLUS PUTORIUS gen. et sp. nov.

This species occurs in the alveoli of the lungs and was found in the British pole-cat, *Putorius putorius*. It was unfortunately impossible to obtain any entire specimens, but sufficient fragments were teased

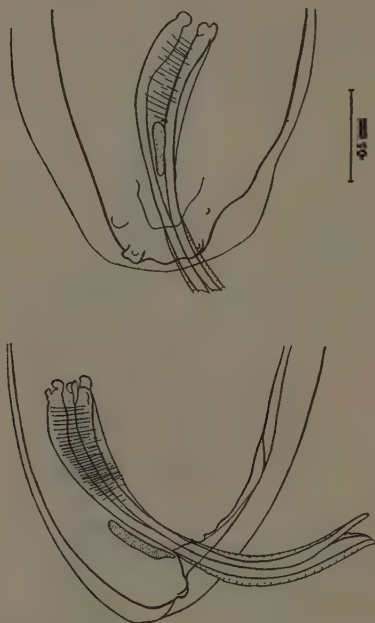


Fig. 10.—*Pseudostrongylus putorius*. Tail of male. Above, ventral view. Below, lateral view.

out of the lung tissue to enable the following description to be prepared :—

The mouth opening, which is a simple pore, is surrounded by six low papillæ. There is no vestibule, and the œsophagus communicates directly with the mouth. The œsophagus is of a simple claviform shape and is about 0.175 mm. long. The nerve-ring surrounds the central region of the œsophagus, and the excretory pore, which is conspicuous, is situated immediately posterior to this. There are no cervical papillæ.

The posterior end of the male terminates in a blunt tail, with no trace of a bursa. There are, however, present a number of low sessile papillæ surrounding the ano-genital opening (fig. 10). A double pair is situated at the extremity and a single pair at the level of the opening. At least one pair of pre-anal papillæ are present.

The spicules, which are 0.225 mm. long, are equal and similar. Each is gently curved and consists of a simple tube terminating in a sharp point. Each spicule is enclosed in a striated sheath, but the finger-like processes of *Protostrongylus* are absent. There is also present a simple gubernaculum, 0.03 mm. long, but there is no trace of a telemon.

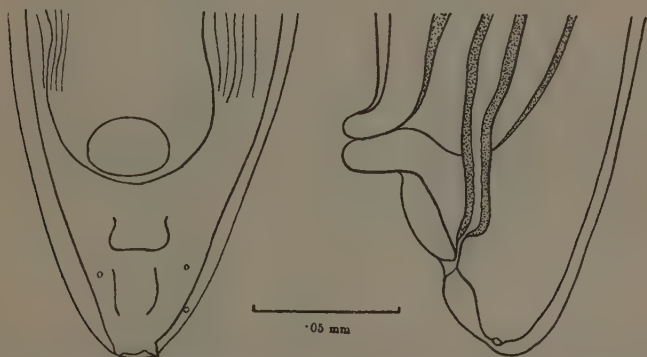


Fig. 11.—*Pseudostrongylus putorius*. Tail of female. Left, ventral view. Right, lateral view.

The female resembles the other members of this group in having a double genital system, which opens in the posterior region of the body in the neighbourhood of the anus. The tip of the tail is blunt and on either side is a small conical papilla. A second pair is found just posterior to the anus, which lies 0.03 mm. from the tip of the tail. The vulva is protuberant and is 0.05 mm. in front of the anus. It communicates with a single long vagina, which in turn joins the two parallel uteri.

The egg is laid in an unsegmented condition and the larva hatches *in situ*. The egg is oval and measures 100μ by 70μ . The larva is 0.33 mm. long and has a small undulating appendix at its posterior end. The anus is 0.3 mm. from the tip of the tail. Six minute circumoral

papillæ are present and the skin is very finely striated. The œsophagus, which is 0.16 mm. long, has only a single terminal bulb, the medial bulb

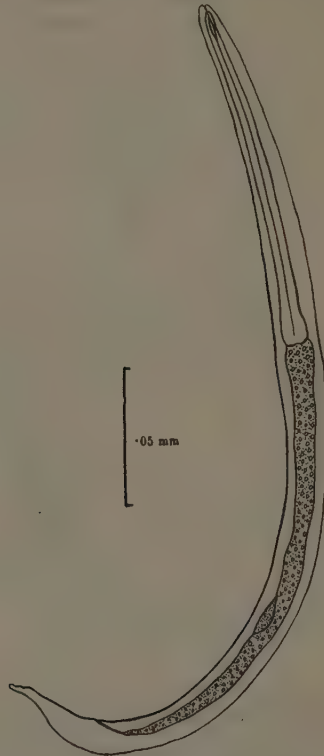


Fig. 12.—*Pseudostrongylus putorius* larva.

seen in the previous species is absent. The intestine is 0.125 mm. long and the genital rudiment is present just posterior to the middle of this.

The larva, while resembling the larvæ of *Protostrongylus* in outline, differs in having a simple œsophagus without a central swelling and in the position of the genital rudiment.

The Mustelidæ are known to be hosts of an imperfectly known species of lungworm *Filaroides mustelorum*, and there was a possibility that this species was related to it.

Fortunately there was available from the frontal sinus of the British weasel (*Mustela nivalis*) several specimens of this form, and from these the following description has been prepared. It is obvious that these species are not congeneric.

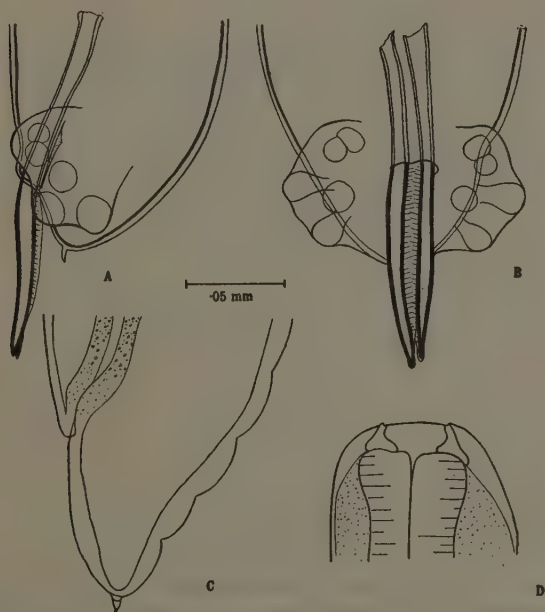


Fig. 13.—*Filaroides mustelorum*. A, tail of male, lateral view. B, ventral view. C, tail of female. D, head.

FILAROIDES MUSTELARUM (Rud., 1819) v. Beneden, 1858.

The oral aperture takes the form of a shallow buccal capsule (fig. 13), the edges of which have a triangular cross section. The apex of this triangle is notched and to the outer projection is attached the cuticle.

The cuticle, except at the extremities, is very thick (fig. 14) and is thrown into transverse annulations, which are, however, only superficial, the inner surface being more or less straight. The thickness of the cuticle in the female amounts to 0.1 mm. and in the male to 0.02 mm. Near the surface it is hyaline, but in its depth it is finely granular and brown in colour. Apart from the junctions of the annulations, there are no transverse striations; the surface is, however, finely mottled.

The cesophagus is about 0.5 mm. long and is only very slightly swollen posteriorly. The nerve-ring and excretory pore lie about the junction of the anterior and middle thirds.

The male is about 9 mm. long. The bursa has been replaced by lateral alæ, each of which is supported by five papillæ. The first and the third of these (counting from the posterior margin) reach the edge of the alæ, while the other three do not. The second papilla appears to terminate on the dorsal surface. The fourth and fifth are very close together. It is possible that these represent the ventral rays, while the other three represent the lateral group of rays of the normal bursa. The second papilla would in this case probably be the equivalent of the externo-lateral ray; while the dorsal rays have disappeared.

The male body terminates in a small cuticular spine (fig. 13A). The spicules are equal and similar and measure about 0.175 mm. in length. They are of the simple tubular type. The anterior end is open (fig. 13), while the posterior end is sharp and pointed. Each carries a spicular sheath which is supported by fingers similar to those found in *Protostrongylus rufescens*. There is no gubernaculum present, but a small wedge-shaped telemon can be seen.

The female genitalia is double and opposed and very convoluted. The vulva is situated at the middle of the body and it communicates with a short vagina which joins a double ovejector (fig. 14), which superficially resembles the *Trichostrongyle* type. The well-marked pars haustrix of that type is, however, absent, and it contains numerous small eggs. From either end run the uteri, which pass almost to the extremities of the worm, reverse and become the very convoluted ovarian tubules.

The anus is situated about 0.08 mm. from the tip of the tail (fig. 13c) and communicates with the rectum by means of a short rectum. The tail, which is blunt, terminates in a small cuticular spike similar to that seen in the male.

Filaroides mustelarum occurs not only in the lungs but also in the frontal sinus and ethmoid bones. The only other nematode described from the frontal sinus was that found in 1920 by Vevers in *Felis bengalensis* and described by him in 1922 under the name of *Trogylostrongylus trogylostrongylus*. That species, however, as suggested by Vevers at the time, does not resemble *Filaroides mustelarum* as it possesses a complete and typical bursa.

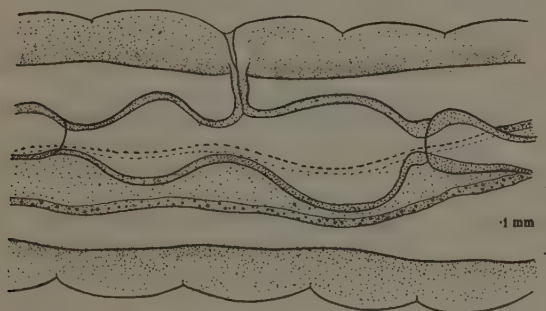


Fig. 14.—*Filaroides mustelarum*. Vulvar region of female.

CONCLUSIONS.

The classification of the Protostrongylidæ has always been a matter of some difficulty, and the splitting of the old *Synthetocaulus* group into its component parts has not entirely removed the difficulties. These are in part due to the simplification of body form which necessarily follows such a specialised habitat as the lungs, blood-vessels and sinuses of the head. There is little doubt that all these forms—*Filaroides* may be a possible exception—were originally bursate nematodes; and to remove from the family such forms as have now lost that bursa secondarily would be to substitute an artificial for a natural system of classification. Accordingly the forms described in this paper are left in the Protostrongylidæ until our knowledge of the classification of the Filarid and Spirurid worms has reached a more satisfactory state.

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***Cylindrogaster coprophaga* gen. et sp. nov. A Nematode
found in a Culture of Fæces from a Wild Brown
Rat.**

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INTRODUCTION.

FREE-LIVING nematodes commonly occur in cultures of fæces, and as Looss (1911) showed years ago they have frequently been mistaken for the developmental stages of parasitic nematodes. For this reason it is important that detailed knowledge of the morphology of such free-living forms should be available. With this end in view the following illustrated account of what appears to be a new genus of nematode has been prepared. The worms occurred originally in a culture of the fæces of a brown rat, *Rattus norvegicus*, made for the study of the free-living stages of the Strongyloides of the rat; and as after detailed study it has been found impossible to find any existing description of nematodes which agree with the structural appearances shown by the worms, it has been decided to create a new genus for their reception.

The principal distinguishing features of the genus are the long pharyngeal rods, which are much longer than those occurring in members of the genus *Rhabditis*, and the first oesophageal bulb, which is muscular in structure and shaped like a cylinder with rounded ends. It is on the appearance of this bulb that the generic name *Cylindrogaster* has been based as it is so distinctive a character in the morphology of the worms.

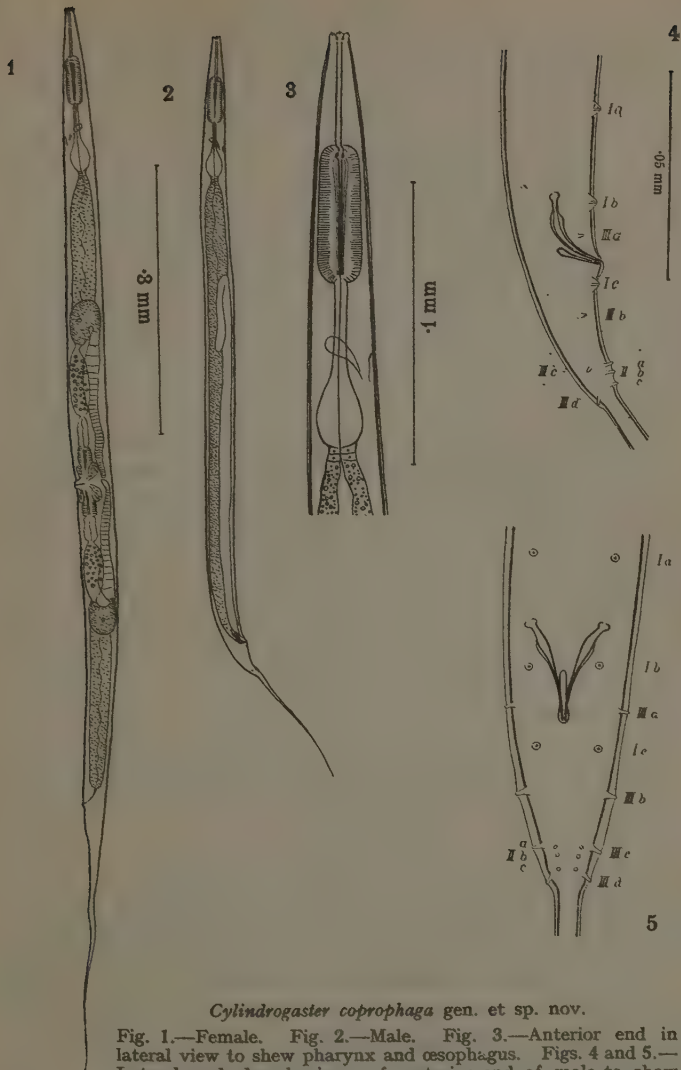
The culture was kept at laboratory temperature, 18° to 20° C., at which temperature the nematodes grew well and multiplied. Sub-cultures from the original Petri-dish culture were successfully made in further supplies of rat droppings and also in cultures made from fæces of guinea pigs and rabbits bred in the laboratory. Sub-cultures were made by breaking down one or two fresh pellets of guinea-pig or rabbit droppings in a small quantity of tap-water so as to yield a moist medium, not too sloppy in consistency. Because of the ability of the worms to grow in such fæcal media the specific name, *coprophaga*, has been given to the worm.

MORPHOLOGY.

As figs. 1 and 2 show, the adult worms of both sexes are fairly long for their breadth; the female, according to the measurements given later, has a length thirty-eight to forty times the breadth, and the male a length thirty-five to thirty-eight times the breadth. Anteriorly the body tapers somewhat and the posterior end in each sex is drawn out into a very long finely tapering tail similar to that found in *Diplogaster longicauda* and *Odontopharynx longicaudata*. It may be noted in passing that out of the large number of specimens examined one, and only one, female has been found possessing a short, bluntly rounded tail terminating the body just behind the anus.

The cuticle shows numerous longitudinal striations, each of which carries extremely fine transverse striæ which are very faint in appearance and are only just discernible under the oil-immersion.

There are six conical lips, each possessing a very small papilla, surrounding the terminal mouth, and the cuticle at the base of the inner face of the lips carries rod-like thickenings, thus making a simple, open buccal cavity. The latter leads into a long tubular pharynx very similar in appearance to the corresponding region in members of the genus *Rhabditis* but much longer. The walls are lined with straight cuticular rods which are slightly knobbed anteriorly. The lumen is narrow and has a width of about one-sixteenth the length of the pharynx. The walls are flexible, as can be seen in living worms and by their frequently becoming folded in fixed specimens. Posteriorly the pharynx leads into the cylindrical muscular bulb of the œsophagus. The cuticular



Cylandrogaster coprophaga gen. et sp. nov.

Fig. 1.—Female. Fig. 2.—Male. Fig. 3.—Anterior end in lateral view to shew pharynx and cesophagus. Figs. 4 and 5.—Lateral and dorsal views of posterior end of male to show shape of spicules and accessory piece, and arrangement of caudal papillæ. In fig. 5 the papillæ, except the lateral ones, have been seen by focussing through the body.

pharyngeal lining is inserted into the anterior end of the bulb for a short distance where it becomes sharply bent ventrally as shown in fig. 3. The cylindrical bulb is almost as wide as the region of the body where it occurs. Its ends are gently rounded and the walls are composed of stout muscles. In specimens fixed by gentle heat, in hot 70 per cent. alcohol or in Carnoy's fixative, the bulb retains its original shape without any distortion, thus revealing the strength of its structure. The lumen runs straight through the bulb and its walls are composed of three cuticular thickenings each of which extends outwards as a lateral flange into the musculature of the bulb for a short distance and appears to be split anteriorly. Between the insertion of the pharyngeal rods at the anterior end of the bulb and the cuticular lining there are short, highly refractive rods.

The second part of the œsophagus consists of a fairly long narrow neck which expands posteriorly into a flask-shaped bulb. The lumen of the neck and bulb has the appearance of a thin straight line and there is no valve apparatus in the bulb. At the junction of the œsophagus and the intestine there is a pair of broad flattened cells on each side of the lumen. The nerve ring crosses the neck of the œsophagus a little anterior to the flask-shaped bulb. The excretory pore and canal are very difficult to make out, but they have been found in living specimens examined under oil-immersion just anterior to the second œsophageal bulb, practically on a level with the nerve ring.

The intestine extends straight from the œsophagus to its termination where it joins the rectum, which opens on the ventral surface of the body.

FEMALE CHARACTERS.—Principal measurements: total length, 1 mm. to 1·34 mm.; greatest breadth, 0·03 mm. to 0·04 mm.; anterior end to vulva, 0·51 mm. to 0·59 mm.; vulva to anus, 0·36 mm. to 0·46 mm.; anus to tip of tail, 0·3 mm. to 0·35 mm.; pharyngeal rods, 0·038 mm. to 0·05 mm.; entire œsophagus, 0·13 mm. to 0·155 mm.; muscular cylinder of œsophagus, 0·055 mm. to 0·07 mm.; neck and second bulb, 0·065 mm. to 0·085 mm.; anterior extent of gonad from vulva, 0·16 mm. to 0·21 mm.; posterior extent of gonad from vulva, 0·153 mm. to 0·21 mm.; distance of lateral post-anal papillæ from anus, 0·032 mm. to 0·034 mm.

The female worms are longer than the males and the tail also is longer. The cuticle at the base of the tail is rather widely separated from the body-wall, but becomes more closely approximated as the tip of the tail is approached. The vulva is situated a little in advance of the middle of the body, as the above measurements indicate. Its lips are rounded and slightly protuberant. It leads into a small chamber connecting the two uteri. The gonads are paired, opposed and reflexed, and the posterior one is frequently a little shorter than the anterior. As fig. 1 shows, the ovary occupies the distal dorsal limb, which often extends beyond the level of the vulva and gradually increases in width until, just prior to the bend, it is sharply constricted and then expands into a swollen portion, which frequently contains a developing egg. This occupies the angle of the bend and a short distance of the proximal limb. Another narrow constriction leads into the large, elongated receptaculum seminis in which small rounded spermatozoa are almost always to be found. There is another constriction of the genital tube, the walls of which now become stout and muscular and the lumen very narrow. This region is to be considered as the uterus, and in mature worms one may occasionally find a single segmenting egg here. The main portion of the uterus is tubular, and for a short distance proximal to the vulva there are well-marked circular muscles in the wall giving it an annulated appearance. In the immediate vicinity of the vulva the uterus walls are provided with two large pyriform muscular masses, one on each side of the mid-ventral line. These muscles may serve to open the vulva and, together with the circular ones already described, no doubt serve as ojectors. Similar pyriform muscles also appear to be present in the same region in females of *Diplogaster longicauda*, and de Man (1912) figures them in the female of *Diplogasteroides spengelii*.

The worms are oviparous and the egg, as occasionally seen in one or other of the two uteri, is partly segmented before being laid. In one fixed worm containing an egg the latter measured 0.046 mm. long by 0.021 mm. broad.

MALE CHARACTERS.—Principal measurements : total length, 0.86 mm. to 0.95 mm. ; greatest breadth, 0.024 mm. to 0.03 mm. ; anterior end to anus, 0.68 mm. to 0.74 mm. ; anus to tip of tail, 0.18 mm. to 0.2 mm. ; pharyngeal rods, 0.36 mm. to 0.5 mm. ; entire cesophagus, 0.11 mm.

to 0.13 mm. ; muscular cylinder of œsophagus, 0.05 mm. to 0.06 mm. ; neck and second bulb, 0.06 mm. to 0.07 mm. ; anterior extent of gonad, 0.42 mm. to 0.45 mm. ; spicules, 0.022 mm. to 0.026 mm. ; accessory piece, 0.012 mm. to 0.013 mm.

The gonad is single and extends anteriorly in the body ventral to the intestine, often reaching from two-thirds to three-quarters of the distance between the anus and the beginning of the intestine. Its anterior end is generally narrow, and in mature specimens is reflexed backwards for a short distance. It is divided into the usual anterior testis and posterior vas deferens.

The spicules are paired, equal and curved. Anteriorly each is rounded and knobbed, following which there is a short part slightly narrower than the knob connecting the latter with the main body of the spicule, which is laterally flattened and shaped like a curved blade with a pointed tip. There is a single accessory piece situated almost at right angles to the longitudinal axis of the worm. When viewed laterally the distal portion appears a little broader than the proximal part, but when seen in dorsal view the latter is seen to be flattened and broader than the points of the spicules as shown in figs. 4 and 5.

There is no bursa and no caudal alæ, but the cuticle in the anal and post-anal region is rather widely separated from the body-wall, being supported by several caudal papillæ arising from the latter. These papillæ are arranged in pairs and have practically the same arrangement and distribution as those occurring on the male tail of *Diplogaster longicauda* as determined by Bütschli (1876) and *Odontopharynx longicaudata* de Man (1912A). Adopting the same system of designation as used by de Man in his description of the last-mentioned nematode, one can arrange the papillæ in three series as follows:—Ia, b, and c consists of three pairs situated ventro-laterally. Of these, Ia and Ib are pre-anal in position, whilst Ic is just post-anal. Ib and Ic are fairly constant in position, but Ia varies somewhat in its distance from Ib. IIa, b, and c consists of three pairs of small papillæ at the base of the tail and lying close to the mid-ventral line. Very frequently the posterior pair, IIc, is separated from IIb by a slightly greater distance than that between IIa and IIb. The cuticle overlying these papillæ is raised up a little ventrally. The third series is more lateral in position

than the other two, and in *Cylindrogaster* there are four pairs of papillæ in the series, whereas in *Diplogaster* and *Odontopharynx* there are only three pairs. They are arranged as shown in figs. 4 and 5, where it can be seen that the pair IIIa is pre-anal, whilst the rest are post-anal in position, III d being distinctly dorso-laterally situated. The additional pair is III c, which is placed fairly close to papillæ IIa and IIb.

SYSTEMATIC RELATIONSHIPS.—In the simple arrangement of the buccal and pharyngeal structures *Cylindrogaster* resembles somewhat *Rhabditis*, but in the elongated pharynx and cylindrical first œsophageal bulb it is quite distinct from that genus. The appearance of this region of the body in *Cylindrogaster* is not unlike the anterior part of the female of *Aulolaimus oxycephalus* as depicted by de Man (1884, Pl. XI, fig. 45), except that in the latter the pharynx alone is longer than the entire œsophagus. Another point of difference is that in the male of *Aulolaimus* the spicules and the caudal papillæ are quite different from those in *Cylindrogaster*.

In possessing female genitalia which are paired, opposed and reflexed the present genus shows a close resemblance to many other free-living nematode genera widely separated systematically, so that on this character alone very little light is thrown on the systematic relationships of the genus.

In the distribution of the male caudal papillæ an arrangement is revealed showing a close similarity to that found in at least two other genera. On this feature *Cylindrogaster* is closely related to *Diplogaster* and *Odontopharynx* two genera which, on the characters of the buccal and pharyngeal regions, are widely separated from it and from each other. It is evident, therefore, that amongst the free-living nematodes we have male caudal characters common to very diverse genera, just as in the animal parasitic nematodes belonging to the order Strongyloidea there are many distinct genera, the males of which possess a bursa having bursal rays arranged on a common plan.

Possibly the arrangement of the male caudal papillæ described above may be considered as a feature of primitive organisation common to the original ancestors of the three genera mentioned. At all events, whether primitive or of later origin (and it seems scarcely feasible that so distinctive a distribution of papillæ should have been evolved inde-

pendently in three different genera), it is worthy of note that the males of these genera possess this feature in common. Assuming that the three genera have sprung from a common stock, we must recognise that in the characters of the mouth and pharynx they have developed on widely differing lines. *Cylindrogaster* has retained a simple mouth and a tubular pharynx; *Diplogaster* has developed a shallow buccal cavity, in which there is frequently a well-defined dorsal tooth; whilst *Odontopharynx* has a deep hollow buccal cavity provided with a dorsal tooth and several ventral and sub-ventral teeth, characters which relate it to such genera as *Oncholaimus*, *Mononchus*, and many other nematodes possessing a cup-like armed buccal cavity.

In attempting to classify *Cylindrogaster* it seems reasonable to place it, for the time being at any rate, along with *Rhabditis*, *Diplogaster* and numerous other genera, in the Family Rhabditidae Micoletzky, 1922, Subfamily Rhabditinae Micoletzky, 1922, as set forth in Baylis and Daubney (1926). The writer regards this arrangement, however, as purely tentative, as in his opinion the present systematics of these genera are in an unsatisfactory condition and need further revision. For example, it is usual to regard the genus *Rhabditis* as a somewhat primitive one. It seems worth while pointing out, however, that though *Rhabditis* may doubtless be considered as exhibiting primitive features in the arrangement of the mouth, the pharynx and possibly also in the shape of the œsophagus, in which characters the first and second stage larvæ of many parasitic bursate nematodes resemble the genus, yet the males in possessing a caudal bursa with distinct bursal rays reveal a specialised feature of organisation, probably more specialised in fact than those nematodes the males of which possess only pre- and post-anal caudal papillæ.

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Observations on the Morphology and Bionomics of *Rhabditis coarctata* Leuck. occurring on Dung Beetles.

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INTRODUCTORY.

DURING the pursuit of field work in the neighbourhood of Warwick in which the collection and examination of insects was involved, it was observed whilst carrying out dissections of dung-infesting beetles that several of them had attached to various parts of the exoskeleton collections of what were at first taken to be fungus spores. On close examination, however, these adherent bodies were discovered to be encysted nematodes which were using the beetles as carrying agents, whereby their transference to fresh dung, required for further development, would be assured.

Our attention was drawn to a short note, written by Christie (1925), in which this author discusses the finding of what was either *Rhabditis coarctata* Leuck. or a closely related species on a number of species of dung beetles in America. With this information in mind, it was decided to culture the worms in order to follow out the life-cycle, determine the species, and make observations on the behaviour of the nematodes in relation to the insects on which they were found attached.

Shortly after the cysts were first discovered the field work was transferred from Warwick to the Institute Farm, and sufficient material was collected to enable further work on the nematodes to be pursued.

Early in May, 1926, a culture was set up which provided sufficient material for the present study.

LIFE-HISTORY.

On an infested beetle passing to a fresh patch of dung the conditions necessary for excystation are attained. The larva then escapes from the cyst and resumes an active life. Feeding is accompanied by growth, and, after a period of time which is probably governed at least in part by the factor of temperature, the adult stage is reached. Following fertilisation the eggs are passed in a segmented condition, larvæ are hatched which live freely in the dung and grow to the pre-encystment stage. Beyond this they are apparently incapable of pursuing their development without some beetle on which they can encyst. Dung beetles feeding on infected fæces tend to collect masses of larvæ which adhere to any portion of the body and form cysts in which the larvæ remain quiescent until favourable conditions for excystation are attained, when the life-cycle is completed.

The Morphology of the Larva previous to Encystment.

Shortly after hatching the young larva shows the main characteristics of the later larval stages. The œsophagus is, however, longer in proportion to the body length and the tail is greatly elongated, the post-anal region being as much as one-quarter of the total body-length. The genital rudiment is even at this stage plainly visible overlying the mid-region of the intestine. The young larva is very active, feeding and growing rapidly until the encysting stage is reached, when it comes to the surface of the dung and, remaining attached by its hinder end, rotates the anterior portion of the body freely in the air. Any moving body passing over the surface of the dung thus collects some of the larvæ, which readily adhere even to a smooth surface such as a needle. At the encysting stage the larva, which is ensheathed, measures from 0.5 mm. to 0.8 mm. in length, by 0.05 mm. to 0.14 mm. in breadth. When encystment is delayed the larva may shrink away from the sheath, which thus extends beyond the head and tail extremities of the worm for as much as 0.04 mm. At the same time the longitudinal ridges of the cyst are formed on the sheath, which remains flexible, the larva retaining both the power of movement and of progression.

The Morphology of the Encysted Stage.

The cysts, when removed from the beetle, appear on general inspection to be of an elongated ovoid form with the posterior or distal extremity of the body flattened and bearing a long spine-like tail. On more detailed examination it is apparent that the cyst is formed of the cuticular sheath of the larva, which, by becoming contracted and folded according to a definite plan, assumes its characteristic shape.

The anterior portion of the cyst, representing the head end of the larval sheath, which serves as the organ of attachment to the beetle, is either cone-shaped or cylindrical. The actual area of attachment consists of a small flattened patch forming either the end of the cylinder or one side of the cone. Thus, although the method by which the larva adheres to the chitin of its host remains unknown it seems probable that this is effected either by means of suction or by the secretion of some adhesive substance at this point. The anterior extremity is followed by a short cylindrical, frequently twisted neck which widens out into the main body mass. This, as stated above, resembles an elongated ovoid structure truncated at the posterior end. This latter appearance is due to a double, sometimes treble, forwardly directed invagination which extends around the sheath just where the body narrows to form the tail. As the invaginations are of considerable depth, a space occurs between each fold of the wall and the succeeding projection. The tail therefore projects freely from the posterior concave surface of the body. When the cysts have been long adherent to the beetle the tail may be broken off, in which case a still closer resemblance to spores of a vegetable organism is produced. In addition to the two or three transverse folds at the posterior end of the body other slighter folds may be present in any region. These vary in number, but when at all well marked rarely exceed four. By means of this system of transverse folding the length of the encysting larva is considerably decreased. Decrease in breadth is effected in a similar way by longitudinal folds. These longitudinal folds extend through the whole body length from the neck region to the proximal portion of the tail. They number from about eighteen to twenty-four around the circumference and show variation in width. They appear as a series of rounded ridges across which the ordinary transverse striations of the cuticle are plainly

apparent. Though less marked than the transverse folds, these longitudinal ridges are yet of sufficient height to give to the margins of the former a distinctly lobed appearance.

Exclusive of the tail, which measures approximately 0.1 mm., the cysts, which show a striking uniformity in size, measure about 0.26 mm. in length by 0.05 mm. in breadth.

Within the folded sheath the larva remains plainly visible extending from the neck region to the posterior transverse folds. It is shrunken away from the cyst wall within which it retains some power of movement. The head region is identical in structure with that of the last stage larva but the buccal rods often show some distortion. The oesophagus, which occupies the majority of the anterior half of the body, is folded in varying degree upon itself. The intestine, which is also bent, is overlaid by a distinct gonadial rudiment of 0.02 mm. to 0.035 mm. in length. The cuticle shows the usual transverse striæ. Within the cyst the larva measures 0.22 mm. in length by 0.03 mm. in breadth.

The Morphology of the Free-Living Larva.

With the resumption of the free-living state, feeding recommences accompanied by growth and a series of ecdyses, the number of which has not yet been definitely ascertained. The essentials of the body-structure remain constant during the larval period, the only changes being a progressive increase in size of the genital rudiment and a shortening of the tail at each ecdysis. A morphological description of a late larval stage may therefore be taken as generally applicable to any of the foregoing phases.

Previous to the penultimate moult the body is slender and elongated, tapering posteriorly to form a short, pointed tail. The anterior end is provided with three large lips, each of which bears a short terminal papilla. Behind the lips, situated laterally, a pair of minute pores with slightly raised margins can be distinguished. These are the external openings of the amphids, which are at this stage particularly distinct, appearing as minute sacs applied to the muscle bands surrounding the buccal region and each communicating with the amphidial pore by means of a slender duct.

The buccal capsule is supported by three longitudinal cuticular rods, which curve slightly outwards as they approach the oesophagus. At

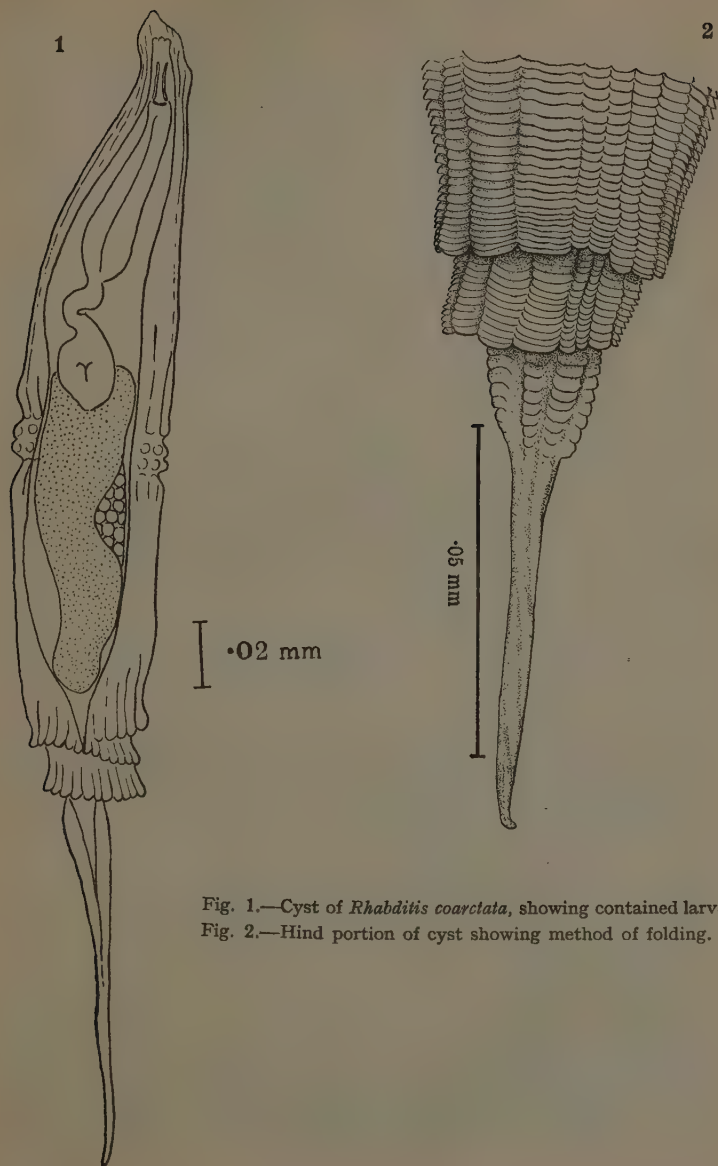


Fig. 1.—Cyst of *Rhabditis coarctata*, showing contained larva.

Fig. 2.—Hind portion of cyst showing method of folding.

their œsophageal end these rods are connected together in a transverse plane by a further series of three rods. These latter are more delicate in structure and together form a ring at the junction of the œsophagus with the buccal capsule. The œsophagus is of the usual double-bulbed Rhabditid type. The first bulb is an elongated pear shape, the second more ovoid and contains a valvular structure. In young larvæ this valve is placed far forward, but in all post-cystic stages it lies approximately in the centre of the bulb. The intestine, which is a simple tube with highly granular walls, surrounds the base of the second œsophageal bulb. It then extends backwards, maintaining a fairly constant diameter, to the posterior end of the body, where it narrows abruptly to form a short straight rectum, opening on the mid-ventral surface a short distance in front of the tail.

The genital rudiment is represented by a syncytial mass overlying the middle two-thirds of the intestine. In some cases either one or both ends may show a slight bending—the beginning of the U-shaped curve. Thus, even at this early stage, some indication of the sex of the larva may be obtained from the gonad, while in the male the anal region is also frequently obscured by a mass of cells which later give rise to the spicular apparatus.

The nerve-cord surrounds the œsophagus in the narrow region between the two bulbs, and opposite it, on the ventral surface, is the excretory pore.

Just previous to the final moult the spicules of the male are apparent and the bursa and bursal rays can be distinguished, folded within the final sheath. In the female the gonads are fully developed and the vulva is visible, but the receptacula seminis, though present, are difficult to distinguish previous to fertilisation.

THE MORPHOLOGY OF THE ADULT.

Female: Principal measurements in millimetres:—

Total body length	0.9	-1.8
Maximum breadth	0.07	-0.11
Length of buccal region	0.025	-0.035
Length of œsophagus	0.15	-0.22
Distance between anterior end and excretory pore	0.1	-0.15
Distance between anterior end and vulva	0.5	-0.97

Ratio, length to breadth	1 : 0.07
Ratio, total length to length of œsophagus	1 : 0.13
Ratio, total length to length of tail	1 : 0.03

The body is elongated and ends posteriorly in a short narrow pointed tail. The mouth is bounded by six large fleshy lips and the amphidial opening is difficult to distinguish. The amphids, nerve ring, excretory pore and alimentary canal correspond morphologically with those of the larva. The gonad consists of a double U-shaped tube opening externally at the vulva, which is situated a little behind the middle of the body. The free end of the anterior gonad lies in the posterior half of the body behind the vulva and may be either straight, U-shaped or still further bent upon itself. It then extends forwards along the dorsal surface to within a short distance of the anterior end of the intestine, where it is recurved towards the ventral surface and passes back to the vulva. From the free extremity for about three-quarters of the length of the dorsal arm the gonad consists of a syncytial mass. This is followed by a cellular region in which the ova go through the processes of maturation and fertilisation. The last portion forms the uterus down which the shelled and segmenting eggs pass to the vulva. The posterior gonad is similar in form and structure to the anterior. The bend of the U occurs far back, just anterior to the rectum. Opposite the vulva the two arms of the uterus unite, forming a common portion.

Lying within the uterus amongst the segmenting eggs and extending back into the region of egg development, a few spermatozoa can be distinguished. These, besides being few in number, are not concentrated in any definite region as is commonly found in free-living nematodes. There is, however, a pair of curious sac-like bodies lying in the region of the vulva and containing masses of spermatozoa, apparently serving the purpose of receptacula seminis. Each of these bodies consists of a rounded sac opening into a wide but tapering duct, which extends towards the vulva, opening at the base of the corresponding vulval lip into the common uterine duct. The sacs extend anteriorly and posteriorly respectively, the anterior lying on the left, the posterior on the right side of the uterus. In young females both the terminal sac and its duct are distended with spermatozoa, but in older forms, when most of the eggs have been shed, though the sac still contains numerous sperms the duct is empty and partially collapsed.

It was found that, by exerting a very slight pressure on the adult worm, any egg which was approaching the vulva could easily be extruded, and further, that with the passage of the egg a certain number of spermatozoa escaped from the sac into the uterus. This was apparently caused by pressure exerted by the egg upon the confined sperms over which it passed, and escape of the sperms from the vulva was then prevented by the immediate contraction of the opening after the extrusion of the egg.

Male: Principal measurements in millimetres :—

Total body length	0.9	-1.05
Maximum breadth	0.06	-0.08
Length of buccal region	0.02	-0.028
Length of œsophagus	0.1	-0.15
Length of spicules	0.08	-0.09
Distance between anterior end and excretory pore	0.09	-0.11
Ratio, length to breadth	1	: 0.06
Ratio, total length to length of œsophagus	1	: 0.1

The male is normally shorter and more slender than the female, and is provided with large straight paired spicules and a distinct genital bursa. The head region and alimentary canal resemble those of the female except that the rectum is obscured by the genitalia. The gonad is single and U-shaped, extending forward from the spicules to within about 0.15 mm. of the œsophagus, where it is recurved. Through the greater portion of its length the gonad is thin-walled and contains masses of developing and fully formed spermatozoa; posteriorly, however, the walls thicken and have a muscular appearance; here no spermatozoa can be distinguished. Each spicule, which is provided with a simple accessory piece, consists of a well-marked rounded knob followed by a stout shaft supporting a pair of flanges. These flanges arise abruptly, one a short distance behind the head, the other further down, and both gradually decrease in size and disappear. The spicules taper and terminate somewhat bluntly. The posterior ventral surface of the body is surrounded by a well-marked bursa supported by ten pairs of bursal rays and a short, stout, papilliform projection which represents the tail. The bursa is a delicate transparent outgrowth with a crenulate margin. It is partially divided by a deep terminal notch into two halves, each consisting of five lobes. There are ten

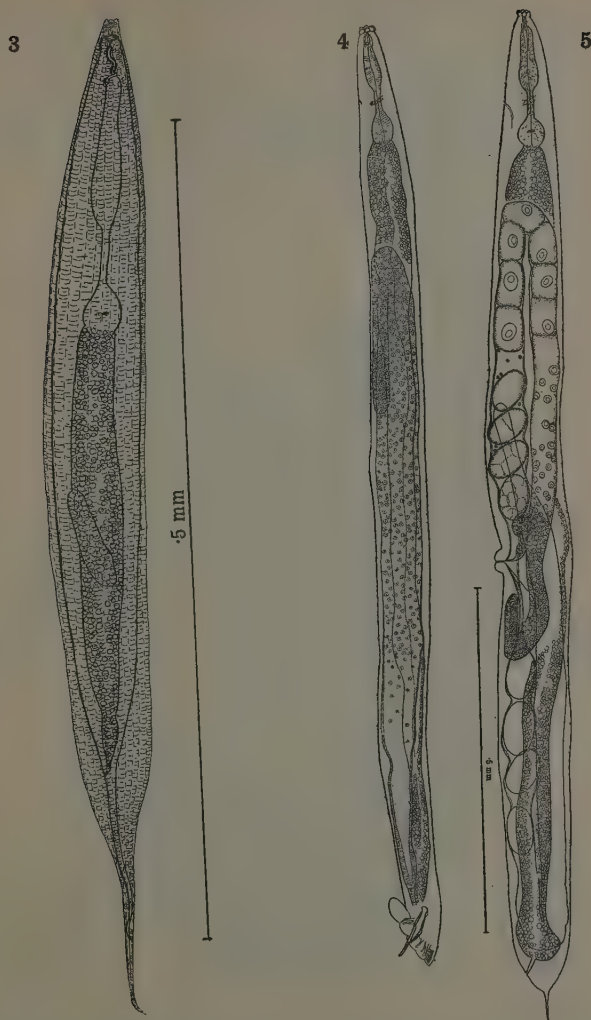


Fig. 3.—Larva previous to encystment, showing contraction within the folded sheath. Fig. 4.—Adult male, showing general morphology. Fig. 5.—Adult female, showing general morphology. Only the anterior branch of the gonad is here shown in detail.

pairs of supporting rays which fall roughly into three groups comprising four, four and two rays respectively. On either side of the terminal region of the body a single ray of medium strength is closely followed by three of extreme delicacy. Just anterior to these are four shorter, stouter rays, and finally, considerably further forward and arising more ventrally, a final pair on either side.

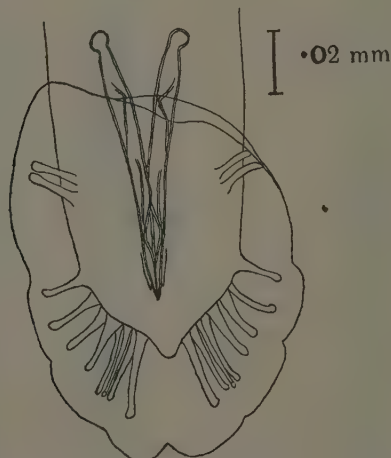


Fig. 6.—Ventral view, tail of male, showing spicules, bursa, and arrangement of bursal rays.

BIONOMICS.

As has been stated above, the material, originally collected at Warwick, was set up as a culture in the early part of May and allowed to remain till October, when detailed work was commenced. When this culture was examined, after the lapse of five months, it was found that the sheep fæces had become quite dried up and contained no nematodes, but three living *Aphodius fimetarius* L., covered with cysts, were extracted. These beetles were then used to start new cultures, using sterilised sheep fæces, and the cysts on them in due course produced larvæ. This point is of some interest when the length of time during which the *Rhabditids* had remained in the cystic stage is considered.



Fig. 7.—Naturally infested *Aphodius fimetarius*, L. bearing encysted *Rhabditis coarctata*.

The naturally infested coprophagous beetles, which were encountered at Warwick, did not bear an excessive number of cysts, and in some cases only very few were found attached to the insect. In beetles, artificially infested by being allowed to remain a week or longer in a sterilised culture swarming with nematodes, the number of cysts found attached was very high, and in several instances practically no part of the legs and upper surface of the insect was free, while a considerable portion of the lower surface also bore cysts. Considering, however, for the moment, a beetle with an average degree of infestation (fig. 7), the points of attachment of the cysts most commonly observed were on the head, especially on the margins of the labrum in species of *Aphodius*, on the edges of the thorax and elytra, and practically always on the leg-joints, but more commonly on the tibiae and tarsi. Other sites, however, which were observed were the palps, antennal joints, especially those of the club in *Aphodius*, all parts of the pronotum, and, at times, the entire surface of the elytra were seen covered with cysts. These clusters of encysted Rhabditids, numbering many hundreds in several cases, had all the appearance of patches of soil or dung adhering to the insect and only on close examination could the cysts, packed closely together, be discerned.

Besides encountering cysts on *Aphodius fimetarius* L., they were also found occurring naturally on *Aphodius punctato-sulcatus* Sturm., *Cercyon impressus* Sturm., *C. melanocephalus* L., *Oxytelus sculpturatus* Gr. and *O. tetracarinatus* Block. Several species of coprophagous coleoptera, collected at the Institute Farm from sheep faeces and introduced into cultures, were artificially infested. These species were as follow: *Aphodius fimetarius* L., *A. proclivius* Brahm., *Oxytelus sculpturatus* Gr., *Tachinus collaris* Gr., *Cercyon haemorrhoidalis* Fab., *Megasternum boletophagum* Marsh., and *Clivina fossor* L.

In order to test the selective tendencies of the larval nematodes, Christie (1925) introduced into a culture several specimens of *Hoplocephala bicornis*, "a beetle which lives under the bark of decaying stumps and logs," and found that cysts were freely formed on these beetles. In our own investigations we repeated this work and found that apparently the Rhabditids had no marked attraction to one host more than another, since, besides encysting on the above-mentioned species of coleoptera,

they also were induced to encyst on several individuals of *Adalia bipunctata* L. and *Coccinella septempunctata* L., both of which do not normally inhabit fæces. In conjunction with this test another was carried out in which certain larvæ were introduced into a sterilised culture containing Rhabditids. After the lapse of a few days the culture was examined and all the larvæ, of which six were Staphilinid, one Lamellicorn (probably that of a species of *Aphodius*), and one Stratiomyid, were found to bear cysts, especially on the head region, thoracic segments and legs.

At the same time, in corroboration of Christie's findings, the formation of cysts was not observed to take place on inanimate objects or on dead beetles, of which the following were used: *Aphodius fimetarius* L., *A. prodromus* Brahm., *Cercyon hæmorrhoidalis* Fab., *Adalia bipunctata* L. and *Timarcha tenebricosa* F.

Cysts formed on living beetles, which subsequently died, still remained capable of producing larvæ when the dead insects were later introduced into sterilised fæces. At the same time beetles, experimentally used to bring about cyst formation, were extracted from cultures and killed, for identification purposes, by being submitted to the fumes of potassium cyanide for an hour. When these insects, thus killed, were then introduced into fresh fæces the cysts still remained capable of producing nematodes, the vapour of the cyanide apparently having no effect on their vitality.

From general observations made on the behaviour of the worms, it seems reasonable to believe that they use the dung beetles upon which they have encysted and which continually fly from one patch of dung to another, as carriers whereby fresh fæces will almost certainly be reached, and thus the life-cycle continued and the species reproduced. Other investigations on the bionomics of the nematodes are contemplated, and whether the continuation of the life-cycle can be effected without the provision of fresh fæces is a matter which is receiving our attention. Culture experiments are being carried out, in order to establish the necessity of a cystic stage during the life-cycle or of the provision of insects on which encystment may occur.

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Some Parasites of Domestic Animals in South-Eastern England.

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INTRODUCTION.

PROFESSOR R. T. LEIPER, F.R.S., was good enough to allow Mr. D. O. Morgan to come to Wye in May, 1926, to initiate me into the methods that the latter has used so successfully in helminth survey work elsewhere. The observations considered in the present paper were begun in this way, and, having been continued since, they form a preliminary account of the occurrence of certain helminth parasites of sheep in South-Eastern England. A record is added of two species recently observed here in pigs. While these records may be of interest for comparison with the results obtained by other workers, it is hoped that they will form the basis for a more detailed survey of helminth parasites in this region. The area that should be covered by such a survey has not been exactly defined; but it would have its centre at Wye and would include not only the interesting country in the immediate neighbourhood, but the important grazing district of Romney Marsh, with its extensive and valuable sheep population (see fig. 1).

This whole area has a very varied topographical and geological structure (see fig. 2). Wye itself nestles at the foot of the North Downs, just at the point where the Great Stour enters the valley which for countless ages as a consequent stream it has been cutting deep into the Chalk formation. To the north, then, lies the Chalk, covered here and there on the top of the Downs with thin patches of Tertiary and Post-Tertiary deposits. All

Cretaceous rocks of the district dip gradually towards the north-east, so that southwards from Wye the geological formations crop out in successively older bands parallel to the foot of the North Downs and varying in width according to the thickness and hardness of the beds. At the foot of the Downs themselves we have the heavy Gault clay succeeded, in order, by the older Folkestone Beds, the Sandgate Beds, the Hythe Beds (which include the siliceous limestone known locally as "Kentish Rag"), the Atherfield Clay and the Weald Clay. Beyond this, and outside the range of our present consideration, are the Hastings Beds. The Kent Coast cuts this succession obliquely, and from Hythe westwards the Hythe Beds stand out above an ancient coastline which we cross in order to reach Romney Marsh, an extensive region of alluvial material reclaimed from the sea by that judicious control of river silting which has been practised in the Marsh from prehistoric times to the present day.

EARLIER WORK.

No exact survey had previously been attempted, but a number of observations have been made from time to time upon the parasitic worms occurring in the neighbourhood of Wye.

Beginning as far back as 1896 references have repeatedly been made by Theobald and Cave, in the *Journal of the South-Eastern Agricultural College*, to the occurrence of helminthic parasites in domestic animals, and it is natural that a considerable number of the cases quoted by these two writers should have reference to occurrences in this district and that information of much practical importance in the treatment of animals suffering from these diseases should have been given from time to time.

Cave and Theobald (1907) record the occurrence of *Ostertagia ostertagi* (Stiles, 1892) Ransom, 1907 (as "*Strongylus ostertagi*") in the stomach of calves in Sussex. The material was identified by Railliet.

At Wye, Gardener (1911) investigated parasitic gastritis, but some of his material came from Taunton. He states that he found *Hæmonchus contortus* (Rudolphi, 1803), *Ostertagia circumcincta* (Stadelmann, 1894), and *Trichostrongylus extenuatus* (Railliet, 1898) in sheep. He indicates that he obtained this last-named species from the abomasum of both sheep and cattle, and in his fig. 4 publishes a photograph, which would appear to be taken from one of his own specimens, shewing the bursa

of the male. This figure agrees with those given by Ransom (1911, figs. 107 to 110, page 95). Gardener also indicates that he met with *Ostertagia ostertagi* (Stiles, 1892) in the fourth stomach of cattle.

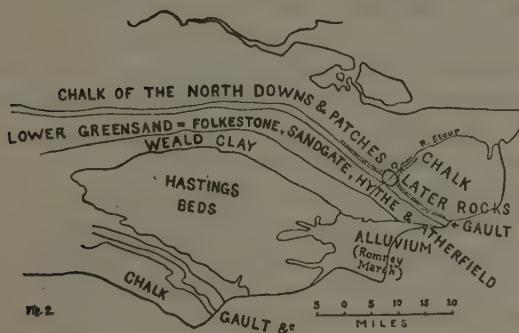


Fig. 1.—Sketch map of South-Eastern England, shewing the distribution of sheep in summer. Each dot represents 1,000 animals. The position of Wye is indicated by means of a ring. This map should be compared with fig. 2. (Adapted from fig. 54 in Hall and Russell, *Agriculture and Soils of Kent, Surrey and Sussex* (1911).

Fig. 2.—Sketch map of South-Eastern England to indicate certain topographical and geological features. The position of Wye is indicated by a ring. (Adapted from the Guide Map in Hall and Russell, *Agriculture and Soils of Kent, Surrey and Sussex* (1911).

Hornby (1914) also worked at Wye and tells us that he met with the following parasites in sheep in this district:—*Hæmonchus contortus*, *Ostertagia circumcincta*, *Trichostrongylus extenuatus*, *Nematodirus fillicollis* (Rudolphi), *Chabertia ovina* (Fabricius), *Trichuris ovis* (Abildgaard). In 36 post-mortems in Kent *O. circumcincta* occurred in twenty-two sheep, *H. contortus* in eight, *N. fillicollis* and *T. extenuatus* each in six, *C. ovina* is recorded once. When the cæcum was thoroughly examined *T. ovis* occurred in the majority of cases.

RECENT INVESTIGATIONS.

The technique employed in this study has been similar to that adopted and described by Morgan (1924).

SHEEP.

The observations below cover the period from May, 1926, to February, 1927, inclusive.

The parasites examined were all obtained in Wye, from a local slaughterhouse or from the College Farm, and, in one case, from a local farmer. Two of the sheep had died, most of the rest were slaughtered for food, while five from the College Farm, which were useless for other purposes, were killed for anatomical demonstrations or for the purposes of helminth study. In all, the alimentary canals of thirty-two sheep and lambs were examined for parasites during the period under review. The examinations have been spread over the whole period, but were more numerous at the beginning than later.

Of the sheep and lambs examined, the source of twenty-four individuals was determined, twenty-three were quite local and one was bought in Ashford market; this last was said to have come from Norfolk; it provided five worms only, three *Hæmonchus*, one *Bunostomum* and one *Cooperia curticei*, the lowest individual count of my series.

The presence of the following helminths in the alimentary canal of sheep has been determined:—

(1) *Bunostomum trigonocephalum* (Rudolphi, 1808) Railliet, 1902.

This species has occurred in the small intestine in May, June, August, September, October, November, January and February, and the largest count was fifty-five, made from a two-year-old Kent sheep purchased in Ashford Market in February. My results tend to confirm the conclusions of Morgan (1925), with regard to the relation that exists between

the occurrence of this form and the age of its host. My first definite record of the appearance of this worm in lambs was in August, when three specimens were found. In October I examined a lamb in which twenty-two specimens were found.

(2) *Chabertia ovina* (Fabricius, 1788) Railliet and Henry, 1909.

This worm has been found in half the hosts examined individually. As early as 18th May, forty-four specimens occurred in the large intestine of a lamb, and nine specimens of the animal occurred in a combined sediment from the first two lambs Morgan and I examined at Wye (killed 11th May, 1926). In none of the sheep examined were more than fifty worms of this species found.

(3) *Oesophagostomum venulosum* (Rudolphi, 1809) Railliet, 1896.

The numbers obtained are very variable, but more than a third of my examinations revealed the presence of this species in numbers varying from 1 to 144. This last figure was reached in a lamb slaughtered on the 14th August.

(4) *Hæmonchus contortus* (Rudolphi, 1803) Cobb, 1898.

Morgan (April, 1924, page 92) cites Boulenger's (1914) statement that this species is common at Wye, Kent. This is borne out by my own experience. More than two-thirds of my examinations revealed the presence of this parasite, and I found it every month during the period under review except in January, when I only made one examination. Of fifteen animals which came from the same farm some two or three miles from Wye during the months of June, July, August, September, October and January eleven were infested, and of these one contained upwards of 1,800 specimens of this animal and five others had upwards of 100 specimens in the abomasum.

(5) *Ostertagia circumcincta* (Stadelmann, 1894) Ransom, 1907.

The species, I find, is common and quite often numerous in the fourth stomach.

(6) *Cooperia curticei* (Railliet, 1893) Railliet and Henry, 1909.

This species has been recognised eighteen times. Once in a sheep in June and again in a lamb in December it was very numerous.

(7) *Cooperia onchophora* (Railliet, 1898) Ransom, 1907.

My record rests upon microscopical examination of one female only which I refer to this species. It was obtained from the small intestine

of a lamb killed 18th May, 1926 (while Mr. Morgan was at Wye). From my notes *Cooperia onchophora* was suspected at the time, evidently by Mr. Morgan.

(8) *Nematodirus fillicollis* (Rudolphi, 1802) Ransom, 1907.

About half my examinations have revealed the presence of this parasite ; ten times it was numerous.

(9) *Trichostrongylus vitrinus* Looss, 1905.

I have not yet made a sufficiently careful study of this and the next species. From preliminary examinations I think that *T. vitrinus* will prove to be a common parasite of the small intestine in our region. As a result of careful microscopic examination I refer female specimens obtained on the following dates to this species :—10th August, 12th August (fair number of similar worms present), 21st September (numerous), 12th October (a few).

(10) *Strongyloides papillosus* (Wedl, 1856) Ransom, 1911.

Morgan identified this species from the small intestine of animals slaughtered at Wye in May, 1926.

(11) *Trichuris ovis* (Abildgaard, 1795) Smith, 1908.

This has proved to be frequent and often numerous, having occurred at least twenty times, while nine times there have been more than fifty specimens present. It occurred each month from May to December inclusive.

(12) *Capillaria longipes* Ransom, 1911.

It has been possible up to the present to confirm the occurrence of this worm in two cases which occurred in August and September. In the former case one female only was seen, but in September several individuals were present. Further study of my preserved material is likely to reveal the presence of this parasite in other sediments.

(13) *Moniezia* spp.

No attempt has been made by the writer to identify the species in the case of this genus. The numbers of parasites found are remarkable from the fact that while specimens were detected nineteen times, and nine examinations each provided but one specimen, and five others revealed two specimens only, the five remaining examinations revealed the following numbers :—3, 3, 5, 16, 48 and 79 respectively. The three

last counts were all in lambs from the same farm about two miles from Wye and were collected in June and July. Specimens of this parasite have been collected each month during the period under review except in January, when only one sheep was examined.

An interesting opinion elicited from Mr. N. V. Hewison, the College Farm manager, in conversation with Mr. D. O. Morgan, was that lambs folded on arable crops suffered less from these parasites than those fed on pasture.

I have kept the eggs of *Moniezia* alive in saline for upwards of three months; at the end of that period an examination of the material shewed moving hooks in a crushed egg, a phenomenon repeatedly observed during the course of the three months.

Three students have recently begun a restricted detailed survey of the surface fauna of pasture with a view to gathering data regarding common forms which might harbour an intermediate host of *Moniezia*.

During Mr. Morgan's stay at Wye he observed and collected *Cysticercus tenuicollis* as well as lungworms indeterminate (either *Synthetocaulus rufescens* or *S. capillaris*).

PIGS.

In December, 1926, I examined four pigs from the Pig Research Station, Wye College, and found that two were infested with nematodes, each with a single species: *Ascaris lumbricoides* (nine specimens) and *Oesophagostomum dentatum* (forty-six examples).

At the present time two students are engaged under my supervision upon the examination of pig faeces for evidence of parasitism by the sieve method suggested by Hall (1911).

ACKNOWLEDGMENTS.

I thank Professor R. T. Leiper, F.R.S., for suggesting this work and for the helpful interest he has shewn from its initiation, when he allowed Mr. Morgan to come to Wye. I am most grateful, too, to Mr. D. O. Morgan, who placed his thorough knowledge of survey work so unreservedly at my disposal at the beginning of the investigation, explaining technical details and, in those first days, indentifying material representative of most of the species recorded in the present paper.

Principal R. M. Wilson and Professor T. W. Cave, F.R.C.V.S., have given me much help and encouragement, and to them, too, I express my best thanks. As this is my first note on helminths I should like to add a word of appreciation of the help of Dr. H. A. Baylis afforded me when I first thought of undertaking some original work on these animals.

SUMMARY.

This paper forms a preliminary account of the occurrence of some helminths parasitic in sheep and pigs in South-Eastern England. The rocks of the Wye district are mainly Cretaceous, while Romney Marsh, with its extensive sheep population, is alluvial. Earlier workers have already considered certain helminthic parasites of this region. The present writer uses Morgan's technique. Thirteen helminths parasitic in the gut of sheep and lambs are listed with notes, and a record is made of some other observations, including the identification of *Ascaris lumbricoides* and *Oesophagostomum dentatum* from swine.

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Observations on the Life History of *Ælurostrongylus abstrusus* (Railliet), the Lungworm of the Cat.

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A PRELIMINARY outline of the life history of the lungworm of the cat and its confusion with that of *Ollulanus tricuspis*, has been given in a previous paper. Since that paper was published, the name of the family of lungworms has been changed to Protostrongylidæ by Professor Leiper; and an examination of adults of the lungworm from the cat, shewed that it belonged to a different genus from the type of the old genus *Synthesocaulus*. To this new genus, the name *Ælurostrongylus* has been given.

Since the publication of the preliminary outline, there has appeared a paper by Sambon, which deals, *inter alia*, with nematodes found in the mouse, and which contains the following statement appended in the form of a footnote to a reference to Leuckart's conception of the life history of *Ollulanus tricuspis*:—"Cameron has recently claimed to have shewn that what Leuckart regarded as the larvæ of *Ollulanus* in mice were in reality those of *Synthesocaulus abstrusus*, a lungworm of the cat. No other worm belonging to the family Metastrongylidæ, of which *Synthesocaulus* is a member, is known to pass through an intermediate host and Cameron's experiments appear to require confirmation."

There can be no possible objection of course to any work being repeated by helminthologists, but the practice of inference by analogy in zoological life-histories is a very dangerous one. Leiper convincingly demonstrated this in his investigations on Egyptian Schistosomiasis. It is a commonplace that *Hymenolepis nana* develops in an entirely different manner from other species of the genus, *Hymenolepis diminuta*, for example. Moreover, there exist at least fourteen genera among the Protostrongy-

lidæ, and of these, one only, *Dictyocaulus*, has been worked out with any degree of completeness; even in this case, there are still many details lacking—a fact which makes, in the case of *Ælurostrongylus*, the danger of inference by analogy even more obvious.

The Morphology of the Larva in the Cat.

The eggs, laid in the alveoli and parenchymatous tissue of the lungs, hatch *in situ* and the larvæ migrate up the trachea, and are swallowed and pass out with the fæces. From the time of hatching until the time that they leave the body in the fæces, no apparent change in morphology takes place.

The larvæ have been allowed to hatch in the dead body of the female *Ælurostrongylus* so that there is no possibility of this being the larval stage of any other species of worms.

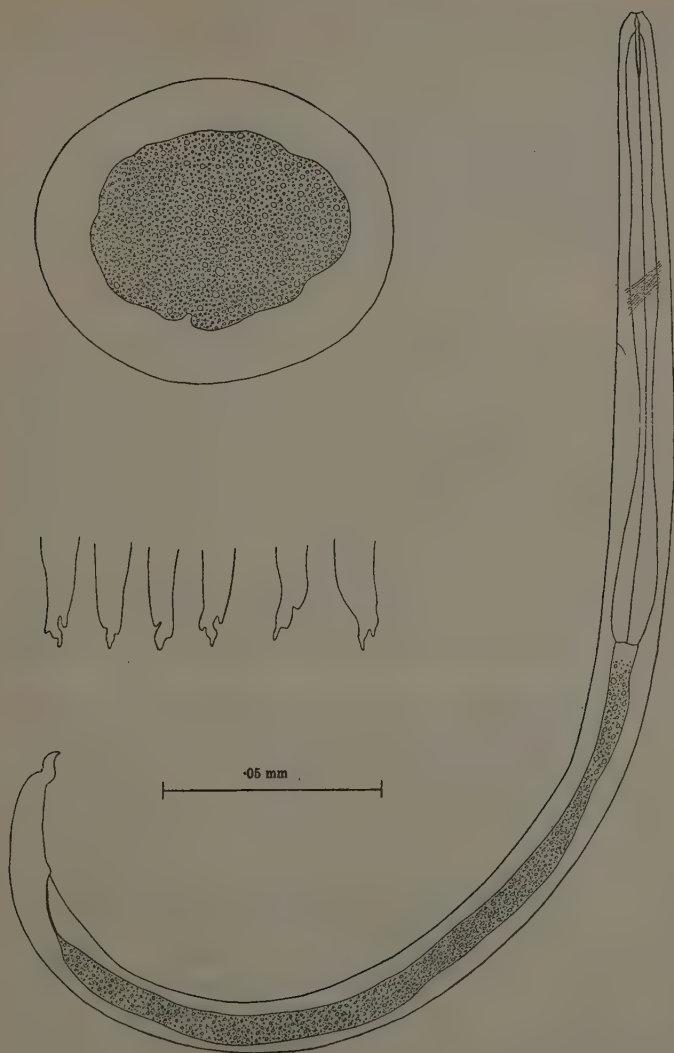
The larva is about 0·36 mm. long and 0·015 mm. broad (fig. 1). The mouth opening is simple and is surrounded by six low papillæ. The cuticle is covered with very fine transverse striations and a double lateral line is seen, suggesting that the first larval stage is omitted in this species.

The œsophagus is 0·14 mm. long and has a central, as well as a posterior, swelling. The anterior part of the œsophagus, terminating at the central bulb, is largely muscular; the posterior portion is distinctly glandular, a characteristic which it shares with the corresponding larval stage of *Muellerius capillaris*. The anterior swelling has a diameter of about 0·006 mm., the posterior swelling, about 0·01 mm., and the narrow part, 0·003 mm.

The œsophagus communicates with the mouth opening by means of a cuticular buccal tube which seems to be continuous with the œsophageal lumen. This tube is dilated centrally (fig. 1) but converges slightly towards its anterior junction with the inflexed cuticle.

The intestine is very granular and measures about 0·19 mm. in length. It is connected with the anus by means of a short cuticular rectum. Just posterior to the anus is a small protuberance which is inconstant in size but is always present. The anus is about 0·03 mm. from the tip of the tail.

The tail is very characteristic and carries an undulating appendix



Ælurostrongylus abstrusus. Fig. 1, Ovum and larva as found in the lungs and intestine of a cat, shewing the variation in tail form.

and normally a dorsal projection. These vary very considerably in size and relative position. That shewn in the larva drawn in fig. 1 is the commonest arrangement, but the six tails shewn above it are all camera lucida drawings of larval tails from the same mother, and this sufficiently illustrates the variations found.

The genital rudiment consists of a small collection of highly granular cells situated just posterior to the middle of the intestine.

The nerve ring is at the level of the anterior bulb of the œsophagus, while the excretory pore is just posterior to this.

Biology of the Larva.

Although larvæ are numerous in the intestinal contents, it was found more convenient to collect them from the lungs. An infected lung was minced, and after mixture with water, the fluid was strained into a centrifuge tube. The precipitate consisted of small particles of lung tissue from which the larvæ could be easily isolated in pure culture.

The larvæ are very active when isolated on a slide from the lung or intestinal contents, and, when collected in water, they still retain their activity. They normally move about with an undulating movement but in a fluid medium make very little forward progress. In mucoid fæcal material, however, they do progress slightly. They do not appear to climb from fæcal cultures in Petri dishes as so many of the Strongyle larvæ do.

Temperature reactions. By means of a Leitz warm stage, the reactions of the larvæ in water to various changes in temperature between 22° C. and 60° C., could be studied. Until 32° C., the normal undulatory movements were observed to become slightly more rapid as the temperature rose. At 37° C., however, they changed to lashing movement, the extremities being very rapidly "whipped" from one side to another. At 40° C., the larvæ commenced coiling and uncoiling, and as the temperature rose a distinct "trembling" was superimposed upon this. At 47° C., the larvæ remained uncoiled but still trembled violently. At 52° C., all movement ceased and did not return again as the temperature fell.

If some larvæ were isolated in water on a slide and a hot needle brought near them, they at first coiled up into a spiral, but as the needle cooled the larvæ uncoiled and moved away from the source of heat.

The reactions of the larvæ to cold were not extensively studied but it was found that although they could exist overnight in an ice chest with a temperature of about 4° C., they were unable to resist actual freezing.

Skin penetration. A number of larvæ were collected in a small drop of water and tested for skin penetration by means of the Goodey Floating Raft technique, the skin of a young rat being used. The larvæ moved actively on the surface of the skin but made no attempt to penetrate it. After the drop of water had evaporated the surface of the skin was covered with egg albumen and when this had dried, the skin was fixed, and serial sections cut. The larvæ could be seen on the surface and none had attempted to penetrate the skin. The saline used for floating the raft was centrifuged, but no trace of larvæ could be discovered. This experiment was repeated with larvæ from the fæces (collected by straining, and decanting and centrifuging) varying in age from one to eight days. In all cases, no larvæ were found to penetrate the skin and it appears legitimate to conclude from this series of experiments that the larvæ are not skin penetrators. On the application of methyl green to larvæ on a slide (as used by Looss in his experiments on the infective larvæ of *Ancylostoma*) the stain did not penetrate the cuticle and the larvæ continued to remain alive, moving their bodies in a slow sideways motion without any forward movement.

Duration of Life. The larvæ do not seem to be able to live in the free state for over a fortnight—the longest period for which the writer could keep them alive in water being eleven days. They appeared to die even earlier in fæces. During their period of free life only degenerative changes were observed and in no case did they shew any sign of further evolution.

Feeding Experiments with Mice. Following the example of Leuckart, these larvæ were fed to a number of tame white mice bred in captivity. All the mice were obtained from the same source originally, although later some were bred in the laboratory. In all forty-six mice were infected, but owing to outbreaks of sarcosporidiosis and of Rat Bite Fever, a number died before the experiments were completed. Such animals have been disregarded. Of the remainder, eleven were examined and were found to have developed cysts, while fourteen were destroyed

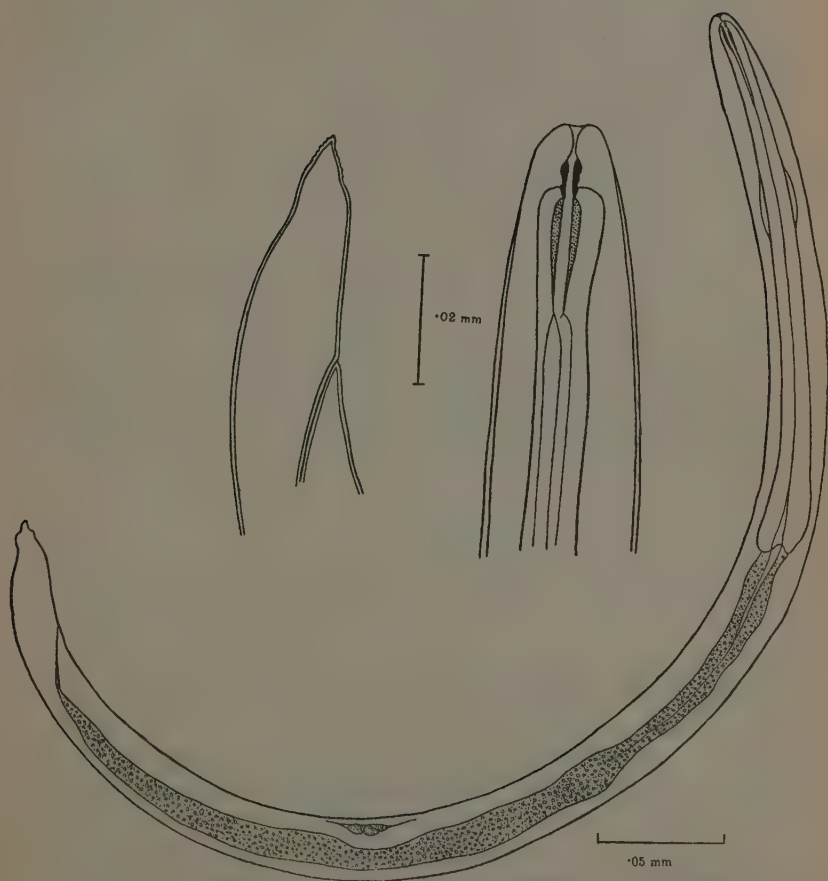
at various dates after infection and preserved pending further investigations into the course of the larva in the mouse. Six mice were found to be negative, so far as could be seen. All these experiments were fully controlled by keeping mice of the same origin and age, uninfected with larvæ of *Ælurostrongylus*. In none of these was any extra-intestinal parasite ever found. In this way, twenty-one control mice were examined. Mice were fed in batches, (a) by feeding on infected embryo-bearing lungs, or (b) by feeding with larvæ isolated from lungs or intestine or stomach placed on moistened biscuit or bread. Care was taken to see that all the material was eaten, but it was not possible to say if every mouse in every batch had swallowed larvæ. It is, therefore, impossible to say whether the six negative results recorded above were due to not being infected, or were slight infections overlooked, or were really failures. Sufficient positives were obtained, however, to make it virtually certain that the larvæ described below are really further stages in the development of *Ælurostrongylus*, a probability more than borne out by subsequent feeding experiments to cats.

The Infective Larva.

It was found that the most convenient way to find if a mouse was infected was to pin the animal on a board with its abdominal surface upward. The skin was then reflected from the inner surface of a hind leg and the underlying areolar tissue examined. The worm-containing cysts were often visible to the naked eye, as "bubbles" lying superficial to the muscles of the leg. Whether so visible or not, a piece of this tissue was removed with curved scissors and placed between two slides and examined microscopically. In this way material was obtained for the following description. If the mouse proved to be infected the remainder was fed to a kitten.

The cysts are about 0.3 mm. in diameter and have a thin fibrous wall. They are filled with a yellow granular or caseous material in the centre of which the larva is seen coiled on itself.

When removed from the cyst the larva is found to be 0.725 mm. long (fig. 2) and about 0.025 mm. in thickness. It is finely striated transversely. The œsophagus is now 0.2 mm. long, *i.e.*, the ratio of the length of the œsophagus to the body length is 1:3.5; whereas in the earlier larva it is about 1:2.5. The central bulb has disappeared



Elurostrongylus abstrusus. Fig. 2, Larva found encysted in the mouse.

and the posterior bulb is relatively smaller. The whole œsophagus is much more muscular and less granular than in the previous stage.

The mouth is a simple pore communicating with the œsophagus by means of a cuticular buccal tube (fig. 2). The buccal tube consists of a more highly cuticularised anterior portion and a less highly cuticularised posterior portion which communicates directly with the lumen of the œsophagus. The anterior portion has a small number of rugæ on its exterior surface while the interior surface is smooth.

The nerve ring is situated about the level of the junction of the anterior and middle thirds, and the excretory pore is just behind this.

The genital rudiment is just posterior to the middle of the intestine.

The intestine is about 0.35 mm. long and is very granular. It communicates with the anus by means of a straight rectum about 0.02 mm. long. The anus is situated about 0.04 mm. from the tip of the tail.

The tail (fig. 2) is bluntly pointed. Towards its tip, the body narrows rather suddenly and the posterior portion is surrounded by deep striations which give it a serrated appearance. There is no trace of the undulating appendix seen in the previous stage.

Experiments on Cats.

The experimental work on cats falls into two groups, (a) feeding with free larvæ from other cats, and (b) feeding with encysted larvæ from mice.

(a) Four cats were fed on various dates with the larvæ isolated from the lung tissue and from the intestine. The first two (E and F) were fed from street infections which were contaminated with *Ollulanus tricuspis*. In these two animals the infection with the latter parasite was demonstrated on post-mortem examination, but in all four (E, F, N and O), no evidence of *Ælurostrongylus* could be seen.

(b) Seven animals were fed at various dates with mice which contained encysted larvæ as described above. Two of these animals died from distemper shortly after infection and no evidence of lung infection could be seen. In the other five, however, *Ælurostrongylus* was found in the lungs. These experiments are detailed below.

Cats B, C and D were procured in Edinburgh in July, 1924.

Cats B and C contained adults of *Ollulanus tricuspis*, together with what Leuckart had considered were the larvæ of this species—larvæ which afterwards proved to be those of *Ælurostrongylus abstrusus*. The lungs were not examined and all other organs except the stomach appeared to be normal. The stomach contained only yellow mucus, and this was scraped off, and, with some of the intestinal contents, was fed to mice a and b. Cultures were made from the stomach and intestinal contents, with and without charcoal; but no larvæ were ever recovered from these. Fæces of both mice were examined the following day, but only *Ascaris* eggs could be demonstrated. These eggs came from the cats and shewed that the mice had actually eaten the material. No larvæ were found in the fæces.

Cat D was secured ten days later. There was a fairly heavy infection of *Ollulanus* in the stomach and larvæ were found, similar to those recovered from the previous cats, not only throughout the alimentary tract, but in the lungs and trachea. The stomach scrapings were fed to mice a, b, c and d, as well as to two kittens, E and F. These cats were subsequently found to have contracted the *Ollulanus* infection but not the *Ælurostrongylus* one.

Four mice had thus been fed on these larvæ and three of these (one died and was preserved) were later examined and found to have encysted larvæ in their subcutaneous tissue; these were fed to cats K and L.

These animals and all others, except those from "street" infections, were obtained as very young kittens and control animals from the same source were retained throughout the series of experiments. In no case, did any of the control animals, including those used in the parallel series on *Ollulanus*, ever display any sign of lungworms.

Cat K, a kitten of four months of age, was fed with mouse b at the end of October, 1924, and destroyed on the 14th January, 1925. The stomach contained no trace of *Ollulanus* adults but the terminal spined larvæ were present in considerable numbers. These were found to be swarming in the lungs. The condition of the animal was emaciated, although it had been feeding well. The stomach contents were fed to cats N and O, but on examination a month and six weeks later, neither *Ollulanus* nor larvæ were found. The lungs were minced and fed to eight mice (g to o), by placing the material in a glass capsule and leaving in the cage with the animals. Four mice later died from *Sarcosporidia*

and no trace of encysted larvæ could be found. The remaining five were destroyed at various intervals and all contained encysted larvæ. These were fed to various clean kittens.

Cat L was fed on the 21st December, 1924, on mice c and d and destroyed a year later. Previous to death, larvæ were obtained from the fæces. The lungs were found to be heavily infected and larvæ in various stages of development were seen. The minced lungs were fed in a manner similar to above, to mice p to u.

Cat P was fed with mice g and h on the 5th February, 1925, and was destroyed on the 24th March of the same year. The lungs were heavily infected with *Ælurostrongylus*, and for the first time, adults were recovered from the lungs. There was no trace of *Ollulanus*. No free larvæ were found although many developing forms were seen in the lungs. This suggests that the parasitic development of the parasite takes about six weeks.

Cat Y was infected on the 18th January, 1926, by feeding on mice j and k. It died on the 18th of March, but the infection was a poor one and only a few larvæ were seen. This animal died from distemper, and this may have affected the normal course of the experiment.

Cat DD was infected on the 19th March, 1926, by feeding on mouse q. It died on the 7th May under circumstances similar to *Cat Y*. No parasites were found in the lungs, although mouse q was known to be infected.

Cat EE was fed with mouse r on the 10th May, 1926, but died ten days later from distemper. It also was negative.

Cat FF was fed with mice s and t on the 5th of June and destroyed on the 7th September, 1926. Larvæ were present in the lungs in small numbers, but no adults were seen on careful dissection. *Ollulanus* was also absent.

Leuckart stated that he found the larvæ encysted, not only in the lungs but also in the diaphragm, the liver and elsewhere in the cat. In spite of careful search and examination of serial sections, I have been unable to find these cysts even in heavily infected cats.

He states that these cysts measure 0.15 mm. to 0.2 mm. and have a thick connective tissue capsule which is often three times the diameter

CATS.

Cat.	Infection.		Examination.		Disposal.
	Source.	Date.	Date.	Result.	
B ...	Street ...	—	11/7/24	+	Fed to mice a and b.
C ...	Street ...	—	—	+	Fed to mice a and b.
D ...	Street ...	—	21/7/24	+	Fed to mice a, b, c and d; and cats E and F.
E ...	Cat D ...	21/7/24	29/8/24	—	—
F ...	Cat D ...	19/3/25	19/3/25	—	—
K ...	Mouse b	23/10/24	14/1/25	+	Fed to mice g, h, j, k, l, m, n and o.
L ...	Mice c and d	21/12/24	19/12/25	+	Fed to mice p, q, r, s, t and u.
N ...	Cat K ...	14/1/25	12/2/25	—	—
O ...	Cat K ...	—	25/2/25	—	—
P ...	Mice g and h	5/2/25	24/3/25	+	Preserved.
Y ...	Mice j & k	18/1/26	18/3/26	+	(Distemper).
DD ...	Mouse q	19/4/26	7/5/26	—	"
EE ...	Mouse r	10/5/26	20/5/26	—	"
FF ...	Mice s and t	25/6/26	7/9/26	+	Preserved.

MICE.

Mouse.	Infection.		Examination.		Disposal.
	Source.	Date.	Date.		
a ...	Cats B and C, and Cat D	11/7/24	23/7/24	?	Preserved.
b ...		21/7/24			
c ...	Cat D ...	21/7/24	23/10/24	+	Fed to Cat K.
d ...	"	"	21/12/24	+	Fed to Cats L and M.
g ...	Cat K ...	14/1/25	5/2/25	+	" " " P."
h ...	"	"	"	+	" " " P."
j ...	"	"	18/1/26	+	" " " Y."
k ...	"	"	18/1/26	+	" " " Y."
l to o ...	"	"	23/3/26	—	No cysts seen.
p ...	Cat L ...	19/12/25	—	—	" " " "
q ...	"	"	19/4/26	+	Fed to Cat DD.
r ...	"	"	10/5/26	+	" " EE.
s ...	"	"	25/6/26	+	" " FF.
t ...	"	"	"	+	" " FF.
u ...	"	"	30/6/26	—	No cysts seen.

of the enclosed space. The larva may completely fill this space with its tightly wound coils or may be surrounded by a slight space filled with a clear liquid.

Recently, Professor Leiper has been conducting a series of experiments with *Trichinella spiralis* and he was struck with the unusual appearance of the cysts in cats caused by the larva of this species. Instead of the usual lemon-shaped cyst so characteristic of mice and pigs, the cyst was almost spherical, although the infection was originally from rats with "normal" cysts. This is obviously because the host reaction in the cat (and examination of cysts from other carnivores, shewed that it is probably a group reaction) differs from that of the rodent or the pig and is not due to there being present a different species of *Trichinella*. These cysts measure about 0.2 mm. in diameter and correspond to Leuckart's description except that the cyst wall is not so thick. As rodents are naturally eaten by cats, it is possible that Leuckart's animal in addition to suffering from *Ælurostrongylus* and *Ollulanus*, also suffered from a *Trichinella* infection. Further work is necessary before this can be definitely assumed, however.

Although there are many essential details of the life history of *Ælurostrongylus abstrusus* still remaining to be elucidated—more especially the development of the larva in the mouse and the development of the adult in the cat—it may be stated that the essential outline of its life history is as follows. The eggs, deposited in the lungs, hatch *in situ*, pass up the trachea, are swallowed, and so reach the exterior with the droppings. There the faeces are eaten by mice and the larva migrates to various situations among the muscles and in the subcutaneous tissue, where, within three weeks, it assumes an infective, encysted form. It may remain viable for at least a year in this situation. If the mouse is now eaten by a cat, the larva escapes from the cyst and, reaching the lungs, within six weeks becomes a mature egg-laying adult.

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Observations on the Life History of *Ollulanus tricuspis* Leuck., the Stomach Worm of the Cat.

By THOMAS W. M. CAMERON, M.A., B.Sc., Ph.D., M.R.C.V.S
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UNTIL recently, it had generally been accepted that the life history of *Ollulanus tricuspis* was a complicated one involving an intermediate host, the mouse. Last year, however, I drew attention to the fact that the larval stages, both in the cat and in the mouse, believed by Leuckart to belong to *Ollulanus*, were really those of *Æluurostrongylus*, the lung-worm of the cat. Subsequent work has enabled some of the details of the life history of *Ollulanus* to be elucidated—although by no means all—and these are considered in this paper.

The Gravid Female.

The adult worms live on the surface of the stomach and in the acini of the stomach glands. In very heavy infections, they may even be found in the first inch of the duodenum but they have never been found beyond the duodenal flexure. This is analogous to the state of affairs seen in other stomach worms in other animals. Their presence on the surface of the gastric mucosa causes the production of a thick glairy mucus which assists in keeping them in position.

In a previous paper on their morphology, I pointed out that they were commonly found with the head bent on itself and subsequent observations have fully confirmed this. They appear to be very lethargic in their movements. All the morphological descriptions in this and the previous paper were made from living specimens taken from the stomach of a freshly killed cat.

General Evolution.

The large granular egg formed in the single uterus gradually develops into a larva (fig. 2), which escapes from the thin eggshell (fig. 3) and subsequently moults—still inside the female—resulting in a form with tricuspid tail. I have not yet discovered the exact stage at which this larva leaves the body, but experiments indicate that this is not the infective stage. The next stage seen is free in the stomach of the cat (fig. 6). Finally, also free in the stomach, is found a stage comparable with the fourth stage larva of the other *Strongyles* (figs. 7 and 10). The sheath of this form, in both sexes, carries a typical tricuspid tail.

All the forms found free in the stomach of the cat—except the adult male—possess a typical tricuspid tail and bear no resemblance whatever to the larva of *Æluurostrongylus abstrusus*.

The first larval stage.

This form is first seen inside the distended eggshell (figs. 1 and 2), but ultimately comes to lie free in the uterus of the female (fig. 3). The description of this and the next stage has been prepared from specimens dissected from the uterus of gravid females.

This larva differs from all subsequent stages in possessing a round blunt tail. It is 0.35 mm. long and about 0.022 mm. in thickness. The mouth opening is a simple pore, apparently not surrounded by circum-oral papillæ. A distinct buccal tube, somewhat dilated centrally, connects the mouth pore with the œsophagus. The œsophagus is about 0.125 mm. long and is of the usual type seen in young strongyle larvæ, *i.e.*, it has a posterior bulb (0.013 mm. in width) joined by a constriction to an anterior swollen portion (0.01 mm. wide).

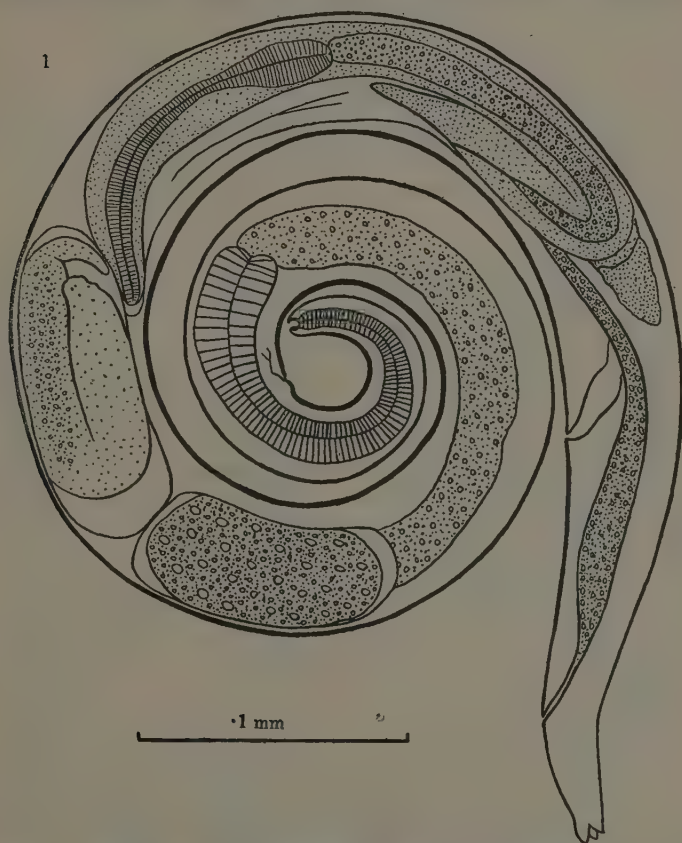
The anterior portion of the body is filled with large granular cells which partly obscure the œsophagus. The intestine is very granular and measures 0.2 mm. long. The anus is situated 0.013 mm. from the end of the blunt tail.

This stage is later seen to become “vacuolated” at both ends and at the posterior end (fig. 4) the tricuspid tail of the next stage may be seen in process of formation.

The second larval stage.

This form is about 0.34 mm. long and has a typical tricuspid tail.

The cuticle is finely striated transversely. The mouth opening is a simple pore which communicates with a buccal tube which is cuticularised



Ollulanus tricuspis. Fig. 1, gravid female shewing egg, developing first stage larva and developed first stage larva. A second stage larva was also removed by dissection from this specimen, but it is not shewn in the drawing.

and is reinforced *anteriorly* with a cuticular ring. It communicates with an oesophagus which is similar in shape to that seen in the first stage and which measures 0.13 mm. in length. The excretory pore

and nerve ring are in the normal place, at the level of the oesophageal constriction. The intestine is very granular and measures 0.16 mm. in length. It communicates by means of a short rectal tube with the anus which is situated about 0.03 mm. from the tip of the tricuspid tail.

The next stage to be described has always been found free in the stomach, but forms apparently similar but measuring 0.4 mm. in length with an oesophagus 0.0125 mm. long, have been dissected from gravid females. It is probable that this is the third stage larva, and as such it is described.

The third stage larva.

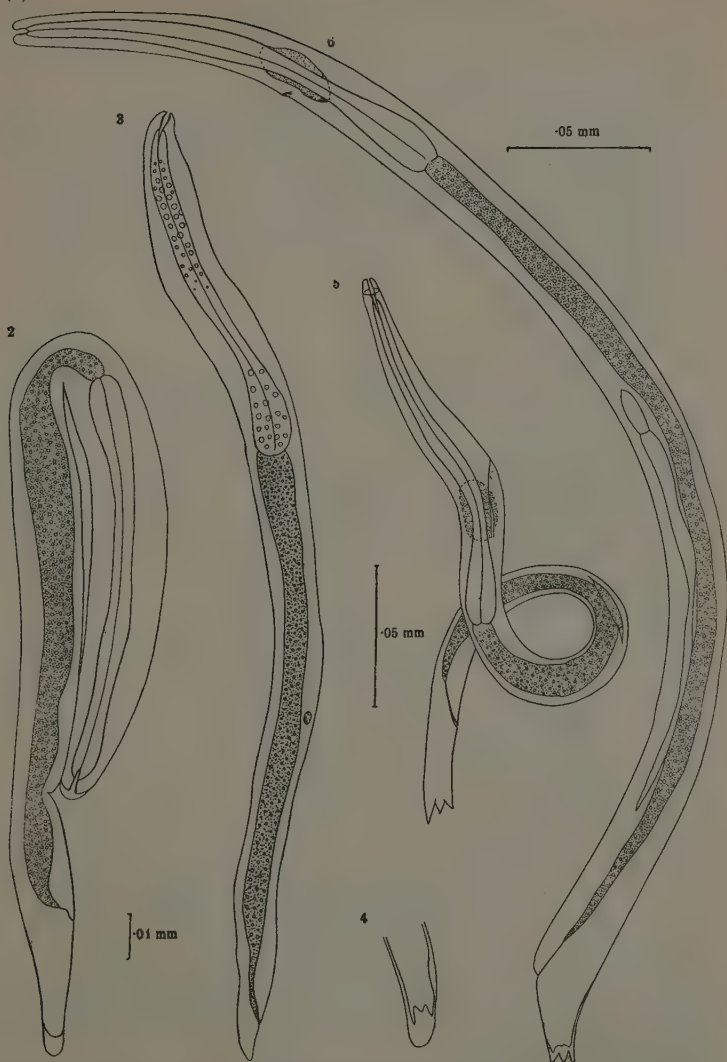
This form (fig. 6) measures 0.5 mm. in length with a width of about 0.022 mm. The skin is finely striated. The mouth opening is simple but it communicates with a V-shaped buccal cavity, the straight sides of which are cuticularised. The oesophagus which still has a slight constriction, is 0.15 mm. long with a maximum width of 0.012 mm. The intestine is very granular and measures 0.35 mm. in length. Towards the posterior portion of the intestine, and running parallel with it, is seen the elongated genital rudiment. There is, of course, still no trace of a genital opening. The anus is 0.03 mm. from the tip of the tricuspid tail.

This form, unlike the adults, usually lies curved like an arc, and is found, not only in the same position as the adults, but free in the cavity of the stomach.

The fourth stage larva.

These are usually found on the surface of the mucosa of the stomach. The sexes are distinct.

The female (fig. 7) is 0.625 mm. long and the oesophagus is 1.4 mm. to 1.6 mm. long, and claviform in shape. The intestine resembles the adult intestine. The mouth opening, in all the specimens observed is undergoing change and the temporary buccal capsule is being replaced by a new one on the anterior end of the oesophagus (fig. 8). The ovary is present as a long tube running forward to almost the level of the beginning of the intestine. Posteriorly it becomes vacuolated and joins a vulva (fig. 9) which does not yet communicate with the exterior. The anus is present in its final position and is joined to the anal opening



Ollulanus tricuspis. Fig. 2, developing first stage larva. Fig. 3, fully developed first stage larva. Fig. 4, tail of larva shewing moulting between first and second stages. Fig. 5, second stage larva. Fig. 6, third stage or infective larva.

of the larval sheath. The sheath and body have the typical tricuspid tail.

The male (fig. 10) is about 0.65 mm. long. The digestive system is similar to that seen in the female. The male genital tube is present as a solid mass running forward from the cloaca, which it appears to join. The temporary anal opening in the sheath was not observed. The bursa (fig. 11) has assumed its final form and spicules and accessory piece are present. The larval sheath is swollen posteriorly, but contracts at its extreme tip to form a tricuspid appendix.

The Biology of Ollulanus.

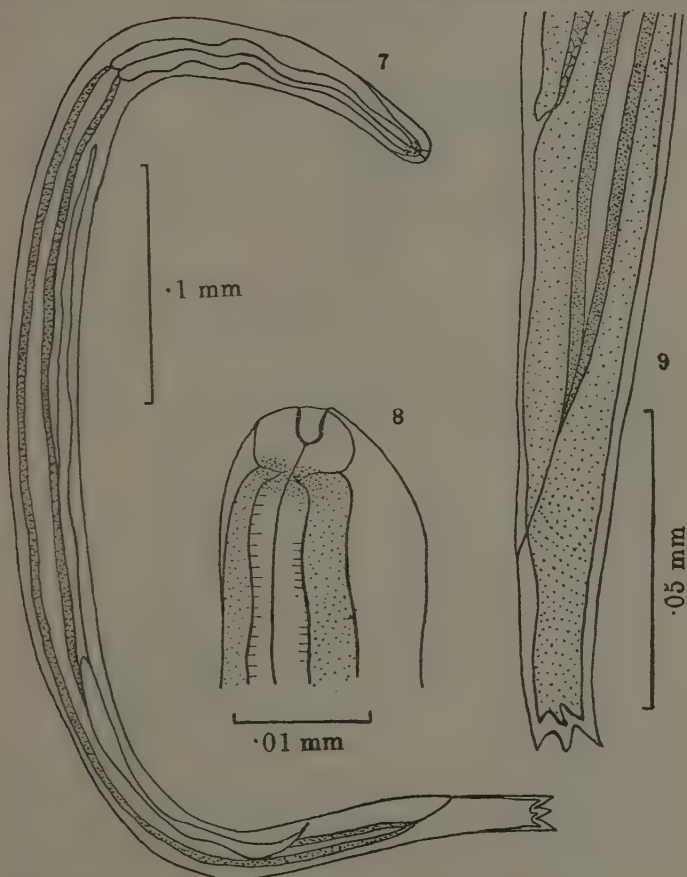
Early in the experimental work, it was found to be comparatively easy to produce a stock infection in cats by transferring the fresh stomach contents of an infected animal to an uninfected kitten by feeding. The question of the natural exit of the parasite was, however, not solved by these experiments. In most animals only two normal routes whereby a parasite may leave the stomach can be found, (a) by passage with the fæces to the exterior, or (b) by remaining in the stomach till after death, when it would be eaten by some intermediate host or even by a definitive host.

Repeated search of the intestinal tract of all the infected cats in this series of experiments failed to reveal any trace of *Ollulanus* larvæ, and the first route did not seem to be the normal one in this case. Experiments with mice, fed not only on the stomach but on the intestinal contents, were also uniformly negative.

In the cat a third possible route may be considered, viz., by emesis. The cat is able to vomit with such facility, and it does so with such regularity—often eating grass to cause emesis—that the action might almost be called a normal one. The parasite, moreover, causes an inflammatory or a catarrhal condition of the gastric mucosa, and such an action would be a natural sequel to this infection. Moreover, cats will readily eat the vomit of other cats, especially if they are hungry, and all natural infections of this parasite which I have seen, have occurred in stray, badly fed animals. Accordingly it was decided to test the possibilities of this route.

Cat S was infected by feeding on an ollulanised stomach, and a few months later was injected subcutaneously with apomorphine (in prefer-

ence to an oral emetic which might have affected the parasite). The animal vomited in a few minutes and a rapid examination of the vomit



Ollulanus tricuspis. Fig. 7, female fourth stage larva. Fig. 8, head of same. Fig. 9, tail of same.

shewed the presence of what has been provisionally called above, the third stage larva. The mass was placed before a kitten (AA), which readily ate it. When this animal was destroyed a few months later, it was found to be heavily infected with *Ollulanus*.

This suggests that infection may be produced by direct feeding of the vomit of an infected animal.

Cat OO was placed in the same cage as Cat S, which was observed to vomit occasionally, and it was given the opportunity of eating the vomited material. When it was destroyed some months later it also was found to have acquired the parasite.

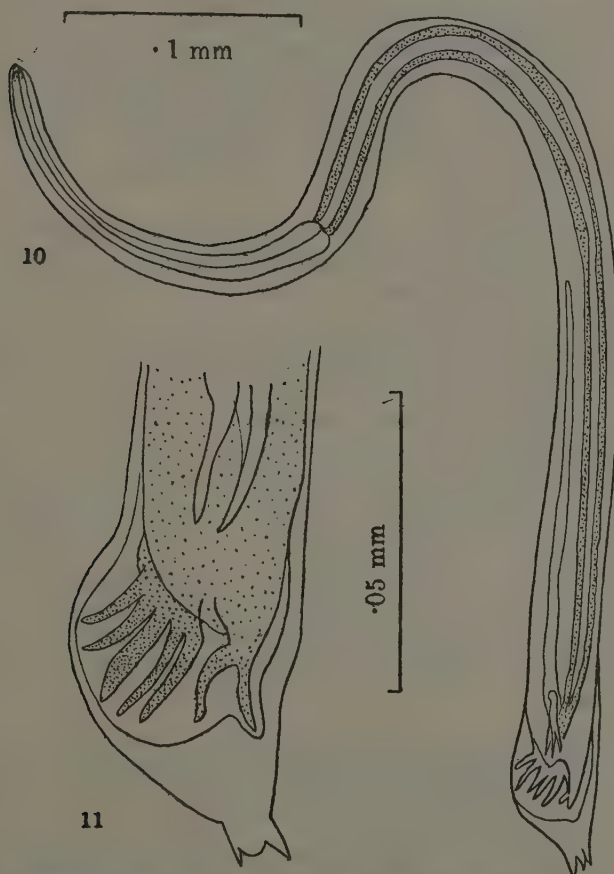
Accordingly it seems probable that emesis is at least one method of conveying the infection from one animal to another; and although it is not claimed that this is the only method of infection, so far no other is apparent.

Cat GG was infected with ten larvæ—similar to those observed in the vomit—and when destroyed six months later was found to have a very heavy infection of fourth stage larvæ and adults of *Ollulanus*. During this period it had been enclosed in a cage by itself and could not possibly have been infected from outside. It seems extremely probable that this is due to continuous auto-infection from the animal's own vomit.

At the same time, it is not possible to entirely exclude the continuous development of the parasite within the host, especially when it is considered that only a very short time need necessarily elapse between the emission of the larvæ in the vomit and their ingestion by another host. In most other parasites a "time factor" outside the body of the definitive host is involved and this seems to be wholly or partly absent in the case of *Ollulanus*. This parasite differs in several important respects from other parasites, not only in its peculiar habitat, but in being viviparous, and in the larvæ completing their preliminary moults within the uterus of the female. It is accordingly not safe to generalize on analogy from other forms having different biological characters. Fülleborn has recently studied *Rhabditis bufonis*, a parasite of the lung of the frog, and he suggests that in this form some substance is produced which would inhibit the continuous development in the lungs. It is possible that such a substance is also produced in this form or otherwise there would be infections even higher than those observed. Or it might be that this substance would only be produced after an optimum concentration of adults in the stomach had been reached.

It is not possible to either prove or disprove either of these hypotheses

at the present moment and this cannot be done until all possibility of continuous auto-infection can be eliminated.



Ollulanus tricuspis. Fig. 10, Male fourth stage larva. Fig. 11, Tail of same.

The development of the parasite inside the stomach has not yet been elucidated, but serial sections of parts of the stomach of several infected cats suggest the possibility of a development *in* the mucosa. There,

superficial to the muscularis mucosa, are seen round-cell accumulations, lying in spherical masses with somewhere or other a pillar of cells communicating with the surface of the epithelium. The whole picture is strongly reminiscent of a tissue reaction following a cell disturbance by developing parasites—somewhat similar to that shewn by *Æsophagostomum dentatum* in the pig, and *Strongyloides stercoralis* in man and other animals. The fact that the parasites are seen deep in the stomach glands gives support to this hypothesis, but hitherto no definite larvæ have been found in these accumulations.

Experiments with Cats.

In the following description of the experimental work with cats, these animals are referred to by capital letters (A, etc.), while mice are referred to by small letters (a, etc.).

Cats A, B, C and D were naturally infected cats procured in Edinburgh. Cat A contained a pure infection of *Ollulanus*; the others had a mixed infection of *Ollulanus* and *Ælurostrongylus*.

Cat A. This cat was examined on the 9th July, 1924, and a slight infection with *Ollulanus* was observed in the stomach. No other parasites—except *Dipylidium*—were found. Cultures were made from stomach and intestinal contents; in all cases the results were negative. The stomach was preserved and no feeding experiments were undertaken.

Cats B and C are discussed in the paper on *Ælurostrongylus* (this Journal, v, pp. 63). Mice were fed on the stomach contents of these two cats and afterwards these were fed to uninfected kittens. Although a typical lungworm infection developed in these cats, there was no trace of *Ollulanus*.

Cat D was also a mixed infection and was used to infect mice as well as two cats (E and F). *Ælurostrongylus* later developed in the cats to which the mice were fed and *Ollulanus* in the cats E and F. In both cases, the infections were pure.

Cats E and F were infected from cat D, and when destroyed one month and eight months later, both were found to be infected with *Ollulanus*. The method of infection was to mince the stomach with a pair of scissors and feed in a glass dish to a hungry cat. Later it was found that such an animal would readily eat unminced stomach and in subsequent experiments it was fed in this way.

The stomach of cat E was fed to cat H and to mice e and f.

Cat H was examined a week after infection and was found to be strongly infected and its stomach was fed to *Cat J*. Unfortunately this animal died from Distemper and was negative on examination.

Cat M was fed with mice e and f, three and a half months after they had eaten part of the stomach of *Cat E*. It was examined four months later and contained no trace of *Ollulanus*.

At this stage the infection ran out and had to be re-introduced from street infected cats.

Cat R was infected by feeding on the stomach of such an animal on 7th October, 1925, and it died ten days later when *Ollulanus* was found in the stomach. These were fed to *Cat S* on the 18th October, 1925. This animal is still alive.

Cat S was injected with apomorphine on the 23rd June, 1926, and the vomit fed to *Cat AA*. Thereafter *Cat S* was enclosed in a cage with *Cat OO* until that animal's death on 10th February, 1927.

Cats T, U and *V* were infected from street sources in January, 1926. The first two were later found to have contracted the infection, but *V* died from gastritis and was negative. The stomach of *Cat T* was fed to *CC* on the 4th May, 1926, while the stomach of *Cat W* was fed to two animals which died from post-distemper gastritis, and were negative.

Cat AA was infected on 27th March, 1926, with the vomit of *Cat S* and destroyed three months later, when it was found to be heavily infected. Its stomach and contents was divided among the five cats, *GG* to *LL*.

Cat BB was infected from street sources and destroyed a month later. It contained numerous specimens of *Ollulanus* and these were fed to *Cat CC*, which, however, died from distemper and was negative.

Cat GG received ten larvæ from *Cat AA* on 23rd June, 1926, and when destroyed was found to contain a very large number of *Ollulanus*.

Cat HH received sixty adults from the same source and when it died a fortnight later, this number was found to have only slightly decreased. The decrease may have been due to methods of searching as the worms are easily overlooked.

Cat II was fed with adults carefully separated from the stomach of *AA* and washed by repeated centrifuging. On its death three weeks later from distemper it was found to be infected ; here again the numbers did not appear to have increased.

Cat JJ was fed with the stomach of *AA* for stock purposes but it died the day after *HH*. The material was refed to *MM*, but when that animal died from distemper several months later the infection had disappeared.

Cat LL was fed with a number of washed gravid females from *AA* which had been "beheaded," so that the animal received only living intra-uterine larvæ and the dead bodies of the adults. No adults developed from this infection.

These last experiments suggest that while adults may be mechanically transferred from one cat to another, and that while third stage larvæ will develop after entering a new animal, larvæ of the first and second stages are not capable of further development except inside the body of the female.

Cat OO, the last of this series, was caged with *S* for some months and permitted to eat the vomit of that animal. On its death, it was found to have naturally acquired an infection.

Controls.

All the cats used in these experiments were obtained as kittens three to four months old from the same source. At the same time about twice this number was obtained for other experiments, and these animals were used to control the *Ollulanus* experiments. In no case was this parasite found in any of the control animals and this makes it practically certain that the experimental cats were free from *Ollulanus* when fed. Thereafter they were confined to cages and accidental infection from outside sources rendered impossible.

The present conception of the life history of *Ollulanus tricuspis* is as follows. The egg hatches in the uterus and the larva which emerges moults *in situ* and its tail changes from a rounded to a typical tricuspid one. The second stage larva develops into a third stage which is found outside the female, but the exact period at which it leaves the mother is still unknown. This form leaves the stomach in the vomit and

is swallowed by a new host in which it develops into a fourth stage larva and finally the typical adult. Some part of this development seems to take place in the depths of the mucous membrane above the muscularis mucosa. It is possible that there are other methods whereby the infective larva may leave the host, but these have not yet been discovered.

Cat.	Infection.		Date of Examination.	Result.	Disposal and remarks
	Source.	Date.			
A ...	Street	—	9/7/24	+	Preserved and cultured
B ...	"	—	11/7/24	+	Also <i>Ælurostrongylus</i> . Fed to mice a & b.
C ...	"	—	"	+	Also <i>Ælurostrongylus</i> . Fed to mice a & b.
D ...	"	—	21/7/24	+	Also <i>Ælurostrongylus</i> . Fed to mice a, b, c, d, & F & G.
E ...	D	21/7/24	29/8/24	++	No <i>Ælurostrongylus</i> . Fed to H, c & f.
F ...	D	"	19/3/25	+	No <i>Ælurostrongylus</i> . Preserved (distemper).
H ...	F	29/8/24	5/9/24	+++	No <i>Ælurostrongylus</i> . Fed to J.
J ...	H	5/9/24	14/9/24	—	No <i>Ælurostrongylus</i> . (Distemper.)
M ...	e & f.	5/1/25	12/5/25	—	No <i>Ælurostrongylus</i> .
R ...	from street	7/10/25	18/10/25	++	Fed to S.
S ...	R	18/10/25	—	++	Atropine, 27/3/26 Vomit to AA.
T ...	from street	4/1/26	4/5/26	++	Fed to CC.
U ...	"	9/1/26	11/1/26	+	Fed to W and X.
V ...	"	"	25/1/26	—	(Gastritis).
W ...	U	11/1/26	18/1/26	—	Fed with 10 adults only. (Gastritis.)
X ...	U	"	26/1/26	—	(Gastritis).
AA ...	S	27/3/26	23/6/26	+++	Fed to GG to LL.
BB ...	from street	2/4/26	4/5/26	+	Fed to CC.
CC ...	T & BB	4/5/26	28/5/26	—	(Distemper).
GG ...	AA	23/6/26	24/2/27	+++	Fed with 10 larvæ.
HH ...	"	"	4/7/26	++	Fed with 60 adults.
II ...	"	"	11/7/26	++	Fed with washed adults.
JJ ...	"	"	5/7/26	++	Fed with stomach.
LL ...	"	"	27/6/26	—	Fed with beheaded adults.
MM ...	JJ	5/7/26	15/12/26	—	(Distemper).
OO ...	S	?	10/2/27	+	Allowed to eat naturally vomited material.

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On *Microstrongylus genettæ* gen. and sp. nov., a Trichostrongyle Parasite of *Genetta senegalensis*.

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A CONSIDERABLE number of specimens of this parasite were collected from the small intestine of a genetie which died in the Gardens of the Zoological Society of London.

The cuticle of the cephalic extremity is dilated anteriorly. This swelling is terminated posteriorly by the cuticle incurving to meet a raised *ring* on the body-wall, about the level of the junction of the anterior and second fifths of the œsophagus. There are no cervical papillæ present, and it is probable that this ring may be regarded as replacing them. Just anterior to the middle of the œsophageal region and at the level of the excretory pore is a cervical *groove* which completely encircles the body. Laterally the cuticle on the anterior margin is thickened; it is also thickened on the ventral side, but less so than laterally. These thickenings are reinforced by a granular inclusion in the cuticle. The posterior margin is thickened only in the region of the excretory pore.

The cuticle is covered with extremely fine transverse striations which are only visible with an oil-immersion objective. These are rather more conspicuous on the cephalic swellings and in the post-anal region of the female. In addition, there are about fourteen longitudinal striations easily visible under the low powers of the microscope. These extend from the posterior margin of the elevated rim which meets the cephalic swelling to the pre-anal region of the female and the pre-bursal region of the male.

The mouth opening is surrounded by six very low-lying papillæ. The œsophagus is about 0.25 mm. long and is only slightly swollen posteriorly (fig. 1). Its maximum diameter is about 0.03 mm. The intestine is typical; as also are the nerve ring and the excretory pore.

The *female* is about 3.5 mm. long with a maximum breadth (at the vulvar region) of about 0.075 mm. The anus is situated about 0.1 mm. from the posterior end, which terminates in a peculiar, dorsally placed "spike" (fig. 2). The anal opening is a transverse slit. The rectum is a short, typical tube which passes anteriorly from the anus almost parallel to the body-wall until it joins the intestine.

The vulva is a typical transverse slit, situated in the posterior region of the body, which it divides in the ratio of 5:1. The vagina is short and directed anteriorly. The ovejectors are of the typical trichostrongyle type and are about 0.2 mm. long; the anterior portion, however, is about twice the length of the posterior. The genital tubes are typical and are only slightly twisted. The posterior tubule turns shortly before the anal region is reached, and it originates in the anterior part of the body. The anterior tubule originates about the same level as the posterior, but proceeds forwards to turn in the neighbourhood of the œsophageal bulb.

The eggs are of typical trichostrongyle type, the average size being 55μ long by 25μ broad.

The *male* is considerably smaller than the female, being only 2.75 mm. long. The bursa is normally folded on itself (fig. 5), when it measures about 0.175 mm. in length and 0.1 mm. across. When opened out carefully its transverse axis becomes 0.27 mm. The *dorsal* ray is bifurcated distally (fig. 4), the internal digitations re-dividing to form a six-pronged fork, the outer prongs of which are bent outwards as in a "trident." Near its base, the stout *externo-dorsal* rays are given off. They terminate some little distance from the edge of the bursa. The *postero-lateral* and the *medio-lateral* rays rise together and proceed parallelly until almost the edge of the bursa. There they diverge slightly to reunite at the extreme edge. They curve dorsally. The *externo-lateral* is shorter and stouter than the others in the lateral group and diverges widely from them from its origin. It terminates some distance from the edge of the bursa. The *ventral* rays are long and slender and

reach the edge of the bursa. They are curved ventrally and proceed parallelly almost to their tip, when they diverge slightly. No pre-bursal papillæ could be seen.

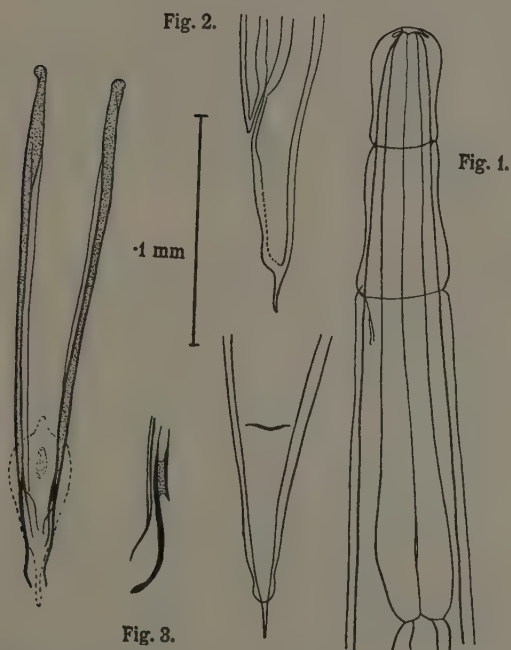


Fig. 1.—Cephalic extremity.

Fig. 2.—Tail of female, lateral and dorsal aspect.

Fig. 3.—Spicules and accessory piece of male.

The bursa is very elastic. The central area is stout and covered with minute bosses. These are absent from the thin, very flexible margin.

The genital valve is typical. There is a very flat genital cone, apparently without ornamentations.

The spicules (fig. 3) are equal and similar. They are long and filiform, the length being about 0.225 mm. Distally they bifurcate. The external limbs are long and undulating; the internal limbs are short and straight and give origin to a third, very slender, hair-like digitation. Each spicule is accordingly tridigitate, although it is only on very close examination that the third termination can be seen.

The accessory piece is about 7.5μ long and of a very peculiar shape (fig. 4). Viewed dorsally, it is shaped like a "snowshoe" with apparently symmetrical centre. Viewed laterally it is seen to be reinforced by a ventral thickening which has a sharp hair-like anterior point. Distally it is very thin and curved towards the spicules. It terminates in a small apical point.

DISCUSSION.

This species belongs to the sub-family Trichostrongylinae Leiper, only two members of which have been previously reported from Carnivores: *Molineus felineus*, recorded by the writer in 1923 from *Felis jaguarundi*, and *Trichostrongylus* (sen. lat.) *patens*, recorded by Dujardin in 1845 from *Fulvorus* spp. The latter species differs materially from this one in size, structure of the head and other features, and although Dujardin's description is not complete in some respects, it is obvious that the two forms are not even congeneric.

This species, however, shows considerable affinities to *Molineus felineus* in several respects. The disposition of the bursal rays and the position of the vulva are very similar in both; while both have an expanded cephalic cuticle and both are very small forms. It differs, however, in other respects, notably in the shape of the spicules and accessory piece, and in the presence of the cervical groove. It is obviously a different species; and the differences in the spicules are so fundamental that the writer considers that it is not related generically to *Molineus*. Accordingly the name *Murostrongylus genellæ* gen. et sp. nov. is proposed for it.

The writer does not consider that it is desirable to attempt to formulate a detailed "generic diagnosis" on the basis of a single species. However, he believes it desirable to draw attention to the points which he considers

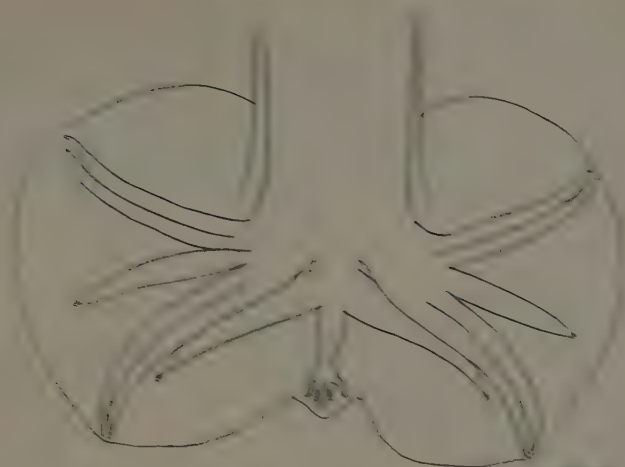


Fig. 4.

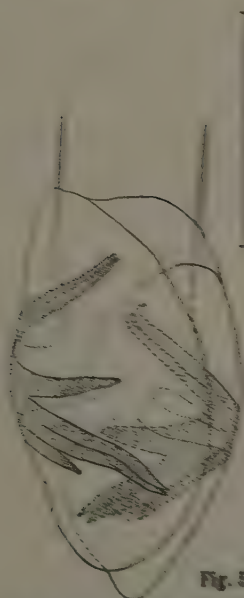


Fig. 5.

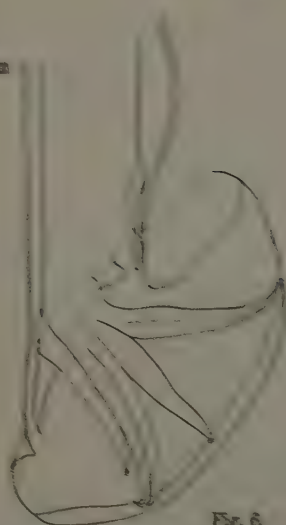


Fig. 6.

Fig. 4.—Bursula spread out. Fig. 5.—Bursula in natural position.

Fig. 6.—Bursula, lateral view.

separate a new genus from others previously existing. In this case these are: the possession of a distinct cervical groove, the swollen cephalic cuticle, the posterior position of the female genital opening, the filiform, tripartite shape of the spicules and the disposition of the bursal rays—especially the externo-lateral. Its affinities to the other trichostrongyline genera are not very obvious; it is, however, most closely related to *Molineus*. The type species is *M. genettæ*.

KEY TO THE GENERA OF THE FAMILY TRICHOSTRONGYLIDÆ LEIPER.

- | | | |
|---|-------------------|------------------|
| A. TRICHOSTRONGYLINÆ (female genitalia double) ... | 1 | |
| 1. Head with umbrella-shaped membrane ... | HISTIOSTRONGYLUS | <i>Molin</i> |
| Head without umbrella-shaped membrane ... | 2 | |
| 2. Spicules, short, with ridges and projections ... | 3 | |
| Spicules, long and filiform ... | 13 | |
| 3. Accessory piece present ... | 4 | |
| Accessory piece absent ... | 10 | |
| 4. Accessory piece ring-shaped; prebursal papillæ absent | ORNITHOSTRONGYLUS | <i>Travassos</i> |
| Accessory piece wedge-shaped; prebursal papillæ | | |
| present or absent ... | 5 | |
| 5. Dorsal lobe of bursa asymmetrical ... | HÆMONCHUS | <i>Cobbald</i> |
| Dorsal lobe of bursa symmetrical ... | 6 | |
| 6. V.V. ray separated from and smaller than L.V.; no | TRICHOSTRONGYLUS | |
| prebursal papillæ ... | | <i>Looss</i> |
| V.V. ray close to and about same size as L.V.; papillæ | | |
| present or absent ... | 7 | |
| 7. Accessory bursal membrane present ... | OSTERTAGIA | <i>Ransom</i> |
| No accessory bursal membrane ... | 8 | |
| 8. Prebursal papillæ; no cephalic dilation ... | HYOSTRONGYLUS | <i>Hall</i> |
| No prebursal papillæ; cephalic dilation ... | 9 | |
| 9. E.L. same size as other lateral rays ... | TRICHOHELIX | <i>Ortlepp</i> |
| E.L. half size of other lateral rays ... | MOLINEUS | <i>Cameron</i> |
| 10. Spicules cleft and barbed; lateral lobes widely | OBELISCOIDES | |
| separated ... | | <i>Graybill</i> |
| Spicules not cleft and barbed; lobes not widely | | |
| separated ... | 11 | |
| 11. Prebursal papillæ conspicuous ... | TRAVASSOSIUS | <i>Khalil</i> |
| Prebursal papillæ absent ... | 12 | |
| 12. Dorsal ray lyre-shaped; spicules with single points ... | COOPERIA | <i>Ransom</i> |
| Dorsal ray like capital of column; spicules with | OSWALDOCRUZIA | |
| multiple points ... | | <i>Travassos</i> |
| 13. Asymmetrical, single cephalic swelling present ... | WARRENIUS | <i>Hall (a)</i> |
| Swelling, if present, symmetrical ... | 14 | |

14.	Vulva in anterior quarter of body	NEMATODIRELLA	
	Vulva in posterior part of body	Yorke and Maplestone	
			15
15.	Bursal lobes asymmetrical	AUSTROSTRONGYLUS	
		Chandler	
	Bursal lobes symmetrical		16
16.	Spicules with multiple points		17
	Spicules with single points		18
17.	Cervical groove present, with cephalic swelling ...	MICROSTRONGYLUS	
		Cameron	
	No cervical groove; no cephalic swelling	GRAPHIDIUM	
		Railliet and Henry	
18.	Vulva close to anus; vagina long	MECISTOCIRRUS	
		Neven Lemaire	
			19
19.	Ventral rays same size and parallel	NEMATODIRUS Ransom	
	V.V. much shorter than L.V. and divergent ...	GRAPHIDIODES	
		Cameron	
B.	HELIGMOSOMINÆ (female genitalia single)		20
20.	Body spirally coiled		21
	Body not spirally coiled		25
21.	Bursa asymmetrical, D. ray replaced by tubercles on E.D.	NEMATOSPIROIDES	
		Baylis	
	Bursa symmetrical, D. ray present		22
22.	Dorsal ray extremely short		23
	Dorsal ray reaches edge of bursa		24
23.	Dorsal ray not split to base	HELIGMOSOMOIDES	
		Hall	
	Dorsal ray split to base	NEMATOSPIRA Walton	
24.	Ventral rays and also M.L. & P.L. united in basal		
	two thirds	VIANNELLA Travassos	
	Ventral rays and also M.L. & P.L. not united in basal		
	two thirds	VIANNAIA Travassos	
25.	Cuticle studded with tubercles	IMPALIA Monnig	
	Cuticle not studded with tubercles	[?]	
26.	Bursa asymmetrical	NIPPOSTRONGYLUS	
		Lane	
	Bursa symmetrical		27
27.	Dorsal ray double	HELIGMOSTRONGYLUS	
		Travassos	
	Dorsal ray with common trunk	HELIGMOSOMUM	
		Railliet and Henry	

- (a) *Warrenius* is provisionally included here on the assumption that *W. bifurcatus* belongs to the same genus as *W. quadricittati* (the type species), the female of which is still undescribed.

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**Studies on the Family *Opisthorchiidæ* Braun, 1901,
with a description of a New Species of *Opisthorchis*
from a Sarus Crane (*Antigone antigone*).**

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INTRODUCTION.

THE classification of the Trematode family Opisthorchiidæ presents some difficulties to the systematist. These difficulties arise partly from the fact that a number of the existing species appear to lack any real morphological characters by which they can be differentiated, slight variations in measurements, together with a difference in host, having been considered sufficient to justify the making of new species. This view has resulted in the placing of undue importance on somewhat minor differences when they do occur in other species, such differences being considered sufficient for creating new genera.

The systematist is further confronted with the difficulty of forming definite opinions on the systematic position of some of the species made by earlier workers. Their descriptions and figures are often inadequate owing to the fact that characters which, in the past, were considered of minor importance are now given much closer attention. Examples of the confusion which has arisen from such a position will be referred to in this paper.

While we are not yet in a position to place the classification of the Opisthorchiidæ on a sound natural basis, a study of the more recently added species and particularly of the new one described in this paper shows that a revision of some of the existing genera is necessary.

ACKNOWLEDGMENTS.

The work has been carried out under the direction of Professor R. T. Leiper, F.R.S., to whom the writer wishes to acknowledge his indebtedness for much helpful advice and criticism.

OPISTHORCHIS DENDRITICUS n. sp.

The material upon which the following description of the new species of *Opisthorchis* is based was obtained from the liver of a Sarus Crane which had died at the Zoological Gardens, London. The writer had no opportunity of examining the specimens when fresh and the measurements are therefore based on preserved material from the helminthological collection of the London School of Hygiene and Tropical Medicine.

The body is long and narrow with its greatest breadth towards the posterior end and gradually tapering anteriorly. It increases slightly in breadth for a short distance between the ventral and the oral suckers and narrows again towards the anterior end, which is truncate. Posteriorly, it narrows from the region immediately behind the testes and ends bluntly. Owing probably to the varying amount of contraction in preserved material the posterior end was observed to be almost conical in some specimens.

The length varies from 8.2 mm. to 15.5 mm., and the greatest breadth from 0.65 mm. to 1.3 mm., measuring 0.4 mm. to 0.8 mm. in the region of the ventral sucker. The cuticle is without spines. The oral sucker is sub-terminal, and measures 0.12 mm. across, which represents an average from the measurement of twenty-three specimens. Similarly the ventral sucker, which is situated in the anterior fifth of the body, has an average measurement of 0.13 mm. The pharynx follows immediately behind the oral sucker and is approximately the same size. The œsophagus varies from 0.36 mm. to 0.6 mm. in length and branches into two narrow cæca, which extend to the posterior end of the body.

The genital organs are situated in the posterior sixth of the body, the ovary being large and multi-lobed and occupying almost the whole width between the intestinal cæca. The receptaculum seminis is also large and pear-shaped and lies in an oblique position immediately behind the ovary with its posterior end towards the right side of the body. This is followed by the testes which are placed almost directly behind one another, and occupy the greater part of the width of the body in this region, overlapping the cæca slightly in some cases. In shape the testes are very deeply lobed—almost dendritic—and show considerable polymorphism (see figs. 2 and 3). The uterus is strongly

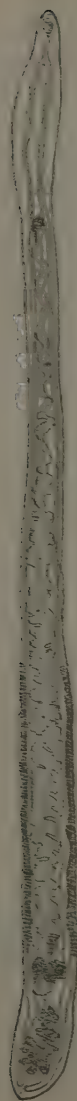


Fig. 1

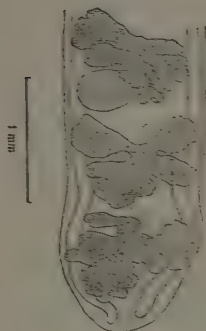


Fig. 2

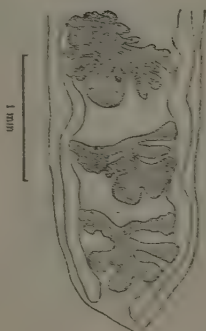


Fig. 3

Opisthorchis dendriticus n. sp.

Fig. 1, shewing entire worm.

Figs. 2 and 3, posterior end shewing genitalia.

developed and occupies the region from the ovary to the ventral sucker and is almost entirely confined between the intestinal cæca. The genital opening is immediately in front of the ventral sucker; a cirrus and cirrus pouch being absent. The vitelline glands lie along the margins of the body and extend from the ovary to a point not more than half the distance from the latter to the ventral sucker. They are not distinctly divided into acini, and in no case have they been found to extend posterior to the ovary. The shell gland is a diffuse organ immediately in front of the ovary. The excretory vesicle is Y-shaped, the stem being distinctly sigmoid and is overlapped on its ventral side by the branches of the testes.

This species is a parasite of the liver of *Antigone antigone* from India. The name proposed for the species is *Opisthorchis dendriticus* n. sp.

SYSTEMATIC POSITION.

O. dendriticus is undoubtedly very closely related to *Notaulus asiaticus* Skrjabin, 1913, from carnivorous birds, and also to *Opisthorchis longissimus* (v. Linst., 1883) from allied hosts. From the former species it differs however in having a sigmoid excretory vesicle which is characteristic of the genus *Opisthorchis*; also in having a multi-lobed ovary, and in the fact that the vitellaria are not divided up into acini and do not appear to extend so far forward as in Skrjabin's species. The testes in both species show considerable polymorphism, but in *N. asiaticus* they do not give the impression of being so dendritic as in *O. dendriticus*. In this respect the affinity seems to be closer to *O. obsequens* Nicoll, 1914, which however is much smaller, and obviously a different species.

O. dendriticus differs from *O. longissimus* in the shape of the testes, which are only slightly lobed in the latter species.

On the whole the new species seems to be more closely related to *N. asiaticus* than to any other, and both should undoubtedly be included in the same genus, i.e., either in *Notaulus* or in *Opisthorchis*. Since however the shape of the excretory vesicle in *O. dendriticus* is similar to that in species of the genus *Opisthorchis* there seems to be no reason for placing it in *Notaulus*. The validity of the latter genus is discussed in the following paragraph.

Genus *NOTAULUS* Skrjabin, 1913.

This genus was created by Skrjabin to include his new species *N. asiaticus* from the liver of *Circus cinereus* and *Aquila imperialis*. He maintained that the separation of several species of the genus *Opisthorchis* into the new genus *Amphimerus* by Barker (1911) had so constricted our conception of the genus *Opisthorchis* that his new species could not be included in it without broadening the generic diagnosis. He further states that his species differs from the typical *Opisthorchis* species in two characters, viz., the size of the testes and the position and shape of the excretory vesicle. In *Opisthorchis* the testes do not occupy the whole width of the body, and lie obliquely behind one another, leaving room for the S-shaped excretory canal to pass between. In *Notaulus*, on the other hand, the testes lie immediately behind one another and fill up almost the whole width of the body, with the result that the excretory canal is pressed dorsally and does not form the S-shaped contour which we find in *Opisthorchis*. Skrjabin compares the character of the excretory canal in *Notaulus* to that in *Clonorchis*

The writer has been able to examine a number of specimens of *Clonorchis sinensis* and finds that, although the branches of the testes overlap the excretory vesicle ventrally, the latter still maintains its sigmoid shape, and in this respect corresponds exactly to the condition found in *O. dendriticus* (see figs. 2 and 3). Skrjabin finds that the excretory vesicle does not show this sigmoid contour in *N. asiaticus*, and if this feature is constant, it would certainly be a point of difference between it and species of the genus *Opisthorchis*. It is however hardly sufficient ground for creating a new genus particularly when the other characters of *N. asiaticus* are similar to the typical *Opisthorchis* species.

Again, the size of the testes cannot be taken as a distinguishing feature in *N. asiaticus* as we find the same condition in *O. longissimus* and *O. dendriticus*.

There seems therefore no reason for the retention of the genus *Notaulus*, and it is considered that *N. asiaticus* should be included in the genus *Opisthorchis*.

Genus *CLONORCHIS* Looss, 1907.

Looss (1907) created this genus to include *O. sinensis* (Cobb., 1875), the chief reason for its separation from *Opisthorchis* being the shape of the testes in this species. At that time there seemed to be every justification for this genus as the dendritic nature of the testes in *C. sinensis* was in marked contrast to the simple or slightly lobed testes in the other existing species of the genus. Since that date, the finding of new species of *Opisthorchis* with testes almost similar to those in *C. sinensis* would seem to make *Clonorchis* of doubtful validity.

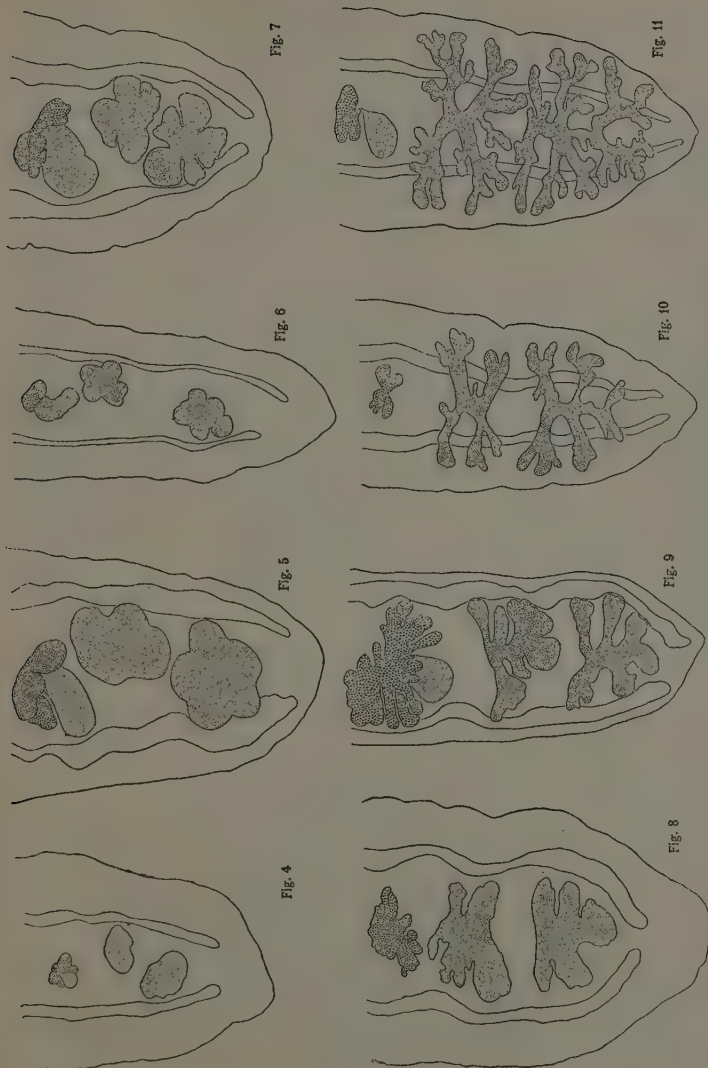
The writer has been able by an arrangement of drawings of species of *Opisthorchis* and *Clonorchis* (figs. 4 to 11), to show a gradual transition from the almost simple, rounded testes in *O. noverca*, to the dendritic testes in *C. sinensis*. Fig. 10, which is drawn from a young specimen of *C. sinensis*, shows that the testes are less ramified than in fig. 11, which is taken from an adult specimen, and forms therefore a connecting link between *O. dendriticus* and *C. sinensis*.

Looss further emphasises the absence of a distinct Y-shaped excretory vesicle in *Clonorchis*. He describes instead a triangular dilation at the anterior end, the two upper angles of which might be considered homologous to the two branches which are found in the excretory vesicle of *Opisthorchis* species. Further, the two main branches of the excretory system in *C. sinensis* arise approximately from the lower angle of this triangle.

This latter character does not form a real distinguishing feature between *Clonorchis* and *Opisthorchis* as a study of the figures given by Ciurea (1915) for *O. felineus* and Stephens (1912) for "*Paropisthorchis*" *caninus* show a somewhat similar condition in the excretory system. In any case, since the dendritic character of the testes in *Clonorchis* is no longer a distinctive feature, the slight difference in the excretory vesicle seems hardly sufficient ground for the retention of this genus.

It is therefore suggested that *Clonorchis sinensis* (Cobb., 1875) Looss, 1907, should be included in the genus *Opisthorchis*.

C. endemicus Looss, 1907, is not generally accepted as a valid species. Kobayaski, 1924, from his study of a large number of specimens of the human liver-fluke in the Far East, has come to the conclusion that there is only one species, viz., *O. sinensis*.



Figs. 4 to 11.—Variations of Testes of *Opisthorchiidae*. Fig. 4, *Opisthorchis nouerca*; 5, *O. geminus*; 6, *O. felinus*; 7, *O. viverrini*; 8, *O. obsequens*; 9, *O. dendriticus*; 10, *O. sinensis* (young stage); 11, *O. sinensis* (adult). Magnifications varied.

Genus *OPISTHORCHIS* R. Bl., 1895.

This genus was split up by Barker (1911) into two genera, *Opisthorchis* s. str. and *Amphimerus*. The validity of the genus *Amphimerus* will be discussed in a later paragraph.

With the inclusion of the species *C. sinensis*, *O. asiaticus* and *O. dendriticus* in the genus *Opisthorchis* the generic diagnosis has to be slightly modified from that given by Barker, as follows:—

Opisthorchiidæ; body distinctly, often very greatly elongated, anterior end attenuated; posterior end broader. Skin generally smooth, without spines. Excretory vesicle usually Y-shaped with long sigmoid stem winding between the testes or passing dorsal to the branches of the latter. Copulatory organs absent. Testes in the posterior portion of the body, and placed either obliquely or directly behind one another; more or less lobed or dendritic. Ovary simple or lobed. Laurer's canal present. Receptaculum seminis prominent. Uterine coils extend from the ovary to the ventral sucker and do not overlap the intestinal cæca to any marked extent. Vitellaria moderately developed, lateral of the intestinal cæca and not extending anterior of the ventral sucker, ending posteriorly at the level of the ovary. Vitellaria form one region.

The genus as emended includes the following species:—

- O. felineus* (Rivolta, 1884) in man, cat and dog.
- O. geminus* (Looss, 1896) in *Milvus parasiticus*, *Anas boschas*, *Circus æruginosus*.
- O. entzi* v. Rátz, 1900 in *Ardea purpurea*.
- O. tenuicollis* (Rud., 1819) in seals, porpoises, dolphins and glutton.
- O. viverrini* (Poirier, 1886) in *Felis viverrinus*.
- O. noverca* Braun, 1903 in man and Pariah dog.
- O. longissimus* (v. Linst., 1883) in *Ardea stellaris*.
- O. simulans* (Looss, 1896) in various carnivorous birds.
- O. piscicola* Odhner, 1902 in *Gymnarchus niloticus*.
- O. obsequens* Nicoll, 1914 in *Hieracidea berigora*.
- O. asiaticus* (Skrjabin, 1913) in *Circus cinereus* and *Aquila imperialis*.
- O. dendriticus* n. sp. in *Antigone antigone*.
- O. sinensis* (Cobb., 1875) in man, cat, dog and pig.

The validity of several of the above species of *Opisthorchis* is still open to doubt and the question can only be settled by extensive feeding experiments to test the specificity of the hosts. In particular, one would refer to the close similarity between *O. felineus*, *O. geminus*, *O. entzi*, *O. tenuicollis* and *O. viverrini*. Slight variations in size are of little value in comparing flukes, particularly with preserved material. Further, one would not attach too much importance to the fact that the above species occur in different hosts. Such widely different hosts as mammals and birds, when feeding on the same intermediate host, may become infected with the same species of fluke.

Genus *AMPHIMERUS* Barker, 1911.

In his new genus *Amphimerus*, Barker (1911) placed six species, previously included under the genus *Opisthorchis*. His genus was made on the ground that the vitellaria in these species are divided into two distinct regions by a break in the line of acini near the ovary—the postovarial portion extending posteriorly to or beyond the posterior testes.

Whether this character can be considered of generic importance is open to doubt, particularly when the genus *Amphimerus* is compared with the genus *Opisthorchis* as modified in this paper. In this case its position appears to be that of a sub-genus in its relation to *Opisthorchis*. The practice of sub-dividing our divisions of classification is, however, undesirable and apt to lead to confusion. In order to avoid this we must be less rigid in our views on the value to be placed on certain characters and it would seem that a certain latitude in the case of the genus is most desirable. If therefore we consider the genus as a group of species which closely resemble a type species there is every justification for retaining *Amphimerus*. The writer considers its retention desirable in the present state of our knowledge of this group.

The species which fall naturally into the genus are :—

A. ovalis Barker, 1911 in turtles.

A. interruptus (Braun, 1901) in *Ardea virescens* and *Alcedo viridiflora*.

A. lancea (Dies., 1850) in *Delphinus tuscus* and *Orcella brevirostris*.

A. pseudofelineus (Ward, 1901) in cat and *Canis latrans*.

A. speciosus (St. & Hass., 1894) in *Corvus americanus*, *Corvus ossifragus* and Egrets.

The species *O. noverca*, which was included by Barker in the above genus, is now placed in *Opisthorchis*. Barker evidently based his decision on the figure given by McConnell (1876) for this species, and he further made a new species *O. caninus* for Lewis and Cunningham's *Distomum conjunctum* (1872). As shown by Leiper (1913) there is little doubt that *O. caninus* (Barker, 1911) is a synonym of *O. noverca* Braun, 1903, and an examination of the more recent descriptions and figures for this species (Stephens, 1912) shows that the character of the vitellaria does not justify its being placed in the genus *Amphimerus*. The writer has observed some slight variation in the extent to which the vitellaria reaches posteriorly in this species. While in some specimens it certainly extends behind the ovary for a short distance, in others it ends anterior to the ovary. In no case, however, can it be said to resemble the true *Amphimerus* type of vitellaria, although somewhat approaching it in some specimens.

Stephens (1912) came to the conclusion that *O. caninus* was not only a distinct species from *O. noverca* but considered that the protrusion of the ventral sucker justified its being placed in a new genus, which he named *Paropisthorchis*. As stated above, this species is the same as *O. noverca* and there is therefore no ground for retaining the genus. As Leiper (1913) in this connection, points out:—"I am forced to the conclusion that the 'pedicle' supporting the ventral sucker is a very variable structure and is really a 'functional' process which happens to have become fixed at death. I have seen similar extrusions of the ventral sucker in certain flukes in the frog when the gut contents are placed in water. The character does not appeal to me as even of specific significance. Its 'generic' value seems inadmissible."

NOTES ON THE OTHER GENERA AND SPECIES OF THE FAMILY *OPISTHORCHIIDÆ*.

The writer has been unable through lack of material to make a complete study of the other genera and species of this family. For completeness, a list of these genera and species is given in this paper together with notes where such are considered necessary.

From a study of the literature and the comparatively few specimens examined there seems to be very slender morphological grounds for separating some of these species, particularly those included in the genus *Metorchis*. Under these circumstances it is exceedingly difficult to

give a key to species of each genus which can be of any value in identification. A key to genera is given together with a list of species and their hosts.

Genus *CYCLORCHIS* Lühe, 1909.

This genus seems to be fairly closely related to *Opisthorchis* and *Amphimerus*, differing chiefly in the fact that the uterine folds in *Cyclorchis* overlap the intestinal cæca. Lühe (1909) considered that the then existing genera *Opisthorchis*, *Clonorchis* and *Cyclorchis* formed a natural group which could be included under the sub-family Opisthorchiinæ. The character of the excretory vesicle and that of the vitellaria in *Cyclorchis* certainly suggest a close relationship with *Opisthorchis*, although Looss (1899) placed the type species *C. amphileucus* in the genus *Metorchis*, which is considered as type of a different sub-family.

The species included in *Cyclorchis* are:—

C. amphileucus (Looss, 1896) in *Naja haja*.

C. campula (Cobb., 1876) in *Platanista gangetica*.

C. campula is placed in this genus by Lühe (1909) as *species inquirenda*. It certainly agrees very closely in many respects with *C. amphileucus*, but unfortunately Cobbold (1876) gives us no indication of the arrangement of the vitellaria which is an important character in the classification of this group of Trematodes.

Genus *METORCHIS* Looss, 1899.

M. albidus (Braun, 1893) in cat, dog, fox, seal.

M. xanthosomus (Creplin, 1846) in domestic duck and various water birds.

M. pinquinnicola Skrjabin, 1913 in *Spheniscus demersus*.

M. crassiusculus (Rud., 1809) in various carnivorous birds.

M. cæruleus Braun, 1902 in *Cairina moschata*.

M. tener Kowal, 1903 in *Mergus merganser*.

M. æsophagolongus described by Katsurada (1914) from the intestine of a cat experimentally fed with cysts from fresh water fish, is not included in the above list. It is difficult to place its systematic position from the description given, but there seems no reason for its inclusion in *Metorchis* when we consider that the excretory pore is terminal and that the vitellaria extend behind the testes. From the figure given, its inclusion in the Opisthorchiidæ is open to doubt, and the habitat is unusual for members of this family.

Genus *PSEUDAMPHISTOMUM* Lühe, 1909.

P. truncatum (Rud., 1918) in dog, cat, wolf, glutton and seal.

P. danubiense Ciurea, 1913 in cat.

Genus *HOLOMETRA* Looss, 1899.

H. exigua (Mueh., 1898) in *Circus rufus*.

H. ægyptiaca Lühe, 1909 in *Circus rufus*.

Genus *PARAMETORCHIS* Skrjabin, 1913.

P. complexum (St. & Hass., 1894) in cat.

P. noveboracensis Hung, 1926, in cat.

Lühe (1909) considered that *Distomum complexum* (St. & Hass., 1894) and *D. conjunctum* (Cobbold, 1860) might be included together in a new genus. Skrjabin (1913) created *Parametorchis* for *D. complexum*, but thought that *D. conjunctum* could not be included with it. The joining of the vitellaria across the anterior end in *D. complexum* and the rosette-like form of the uterus round the ventral sucker certainly seem in marked contrast to that obtaining in *D. conjunctum* as far as can be made out from Cobbold's figure (1861). One must, however, allow a certain latitude for the descriptions and figures of the older writers, and rather than create a new genus for this species it is suggested that *D. conjunctum* should at present be placed in *Parametorchis* as *species inquirenda*.

This view gains support from a consideration of the species recently described by Hung (1926), which is named *Parametorchis noveboracensis*. In this species we find some characters resembling *P. complexum* and some *D. conjunctum*. It is similar to *P. complexum* in having a rosette-like uterus round the ventral sucker, while in the absence of a commissure connecting the anterior ends of the vitellaria it comes close to *D. conjunctum*. Unfortunately, Hung makes no comparison between his species and *D. conjunctum*; his description and figure, however, show that they are sufficiently alike to be included in the same genus.

Genus *MICROTREMA* Kobay, 1921.

M. truncatum Kobay, 1921 in pig.

Genus *PACHYTREMA* Looss, 1907.

P. calculus Looss, 1907 in *Larus ridibundus* and *L. argentatus*.

P. magnum Trav., 1921 in *Sterna magna*.

P. proximum Trav., 1921 in *Heterophygia fuscicollis*.

Genus *DIASIA* Trav., 1923.

D. diasi Trav., 1923 in *Plotus anhynga*.

Having regard to the unique habitat of *Ratzia parva*, it seems doubtful if the genus *Ratzia* should be included in the family Opisthorchiidae. Stossich (1904) states that this fluke was found in small cysts above the lumbar muscles of *Rana esculenta*. It may be that we are here dealing with a fluke which has found its way into an abnormal host as almost all the Opisthorchiidae are found in the liver and gall bladder of their hosts. While the arrangement of the genitalia and the sigmoid excretory vesicle certainly place this species in the Opisthorchiidae, it would certainly seem more reasonable in view of its habitat to consider *Ratzia* as a *genus inquirendum* until further data are obtained.

One might also mention as *species inquirenda*, *Distomum sulcatum* v. Linst., 1886 from *Perdix græca*. Neither the description nor the figure are adequate for determining its systematic position. The extent to which the uterine folds extend anterior to the ventral sucker suggests a *Metorchis* species, but the confining of the vitellaria to the middle of the body is similar to the condition found in *Opisthorchis*.

GENERAL REMARKS.

Altogether, with the exclusion of *Notaulus* and *Clonorchis* there remain ten genera in the family Opisthorchiidae. Poche (1926) gives twelve as the total after including the two above genera and *Ratzia*. It would seem from his remarks that he has omitted one of the two recently added genera, *i.e.*, *Microtrema* or *Diasia*.

The grouping of these genera into sub-families on the basis of a natural relationship is exceedingly difficult. While *Opisthorchis*, *Amphimerus* and *Cylorchis* fall together into the sub-family Opisthorchiinae as outlined by Lühe (1909), *Pachytrema* and *Diasia* into Pachytremineæ Railliet, 1919, the remaining genera do not lend themselves easily for classification. It might be reasonable to place *Metorchis* and *Pseudamphistomum* together into the sub-family Metorchinae on the ground that the excretory vesicle opens ventrally in the species of these two genera. *Parametorchis*, *Holometra* and *Microtrema*, on the other hand, have characters so distinctive that each could form the type genus of a new sub-family.

Neither the arrangement of the vitellaria nor the character of the

excretory vesicle can be used as a basis for grouping the genera as this would tend to bring together genera which, on general grounds, should be separated. An instance of this is *Parametorchis* which, having a sigmoid excretory vesicle, could be placed near *Opisthorchis*, and on the arrangement of the vitellaria near *Metorchis*. Again, *Microtrema* as Kobayashi (1921) points out, has a much thickened body suggesting a relationship with *Pachytrema*, while the arrangement of the internal organs brings it near *Pseudamphistomum*. *Holometra*, owing to the grouping of the vitellaria in the anterior end, is also quite distinctive.

It is considered therefore that, in the present state of our knowledge, no satisfactory grouping into sub-families can be made. The erection of an artificial classification would be of little value, even on the ground of convenience.

The addition of the genera, *Pachytrema*, *Diasia* and *Microtrema* to the Opisthorchiidæ has somewhat altered our conception of this family. These genera contain species which have thick rounded bodies and are therefore in marked contrast to the other species of this group which have flat thin bodies. These genera might even be considered sufficiently distinctive to be placed in a new family. At present their retention in the Opisthorchiidæ may perhaps be more reasonable; the family diagnosis is therefore emended, as follows:—

Body generally flat and transparent; sometimes much thickened, narrowing anteriorly. Suckers near each other (except in *Microtrema*), often only moderately developed or atrophied. Pharynx present and usually followed by a short œsophagus. Intestinal cæca long and unbranched, not always reaching the posterior end. Excretory vesicle Y-shaped with proportionately long stem and short branches, opening at the posterior end or on the ventral surface in the region of the testes. In the former case the stem winds S-shaped between the testes or may lie dorsal to the testes. The genital opening is immediately in front of the ventral sucker. A cirrus sac is absent. The testes lie near the hind end of the body, obliquely or directly behind one another; sometimes they lie laterally. They are simple, lobed or dendritic. The ovary lies immediately in front of the testes and may be simple, lobed or multilobed. Laurer's canal present; receptaculum seminis usually strongly developed. Vitellaria moder-

ately well developed, divided into acini or continuous and lie between the cæca and the margins of the body. Uterine folds in front of the testes and mostly in front of the ovary, extending to or in front of the ventral sucker. Eggs numerous, small and light brown in colour. Habitat:—In the gall bladder and bile ducts of mammals, birds, reptiles and fish.

KEY TO THE GENERA OF THE FAMILY OPISTHORCHIIDÆ.

Opisthorchidæ with flat, thin body	2
Opisthorchidæ with thick, slightly flattened body ...	3
2. Vitellaria not extending anteriorly beyond the ventral sucker	3
Vitellaria extending anteriorly beyond the ventral sucker	5
3. Vitellaria not extending posteriorly to the testes ...	4
Vitellaria extending posteriorly to, or beyond the posterior testes	AMPHIMERUS
4. Uterine folds confined between the intestinal cæca ...	OPISTHORCHIS
Uterine folds overlap the intestinal cæca	CYCLORCHIS
5. Excretory vesicle opens at the posterior end	6
Excretory vesicle opens on the ventral surface	7
6. Vitellaria entirely confined to the region in front of the ventral sucker	HOLOMETRA
Vitellaria not entirely confined to the region in front of the ventral sucker	PARAMETORCHIS
7. Excretory vesicle terminates in a pseudo-sucker ...	PSEUDAMPHISTOMUM
Excretory vesicle terminates in a simple opening ...	METORCHIS
8. Uterus in front of the ventral sucker	MICROTREMA
Uterus behind the ventral sucker	9
9. Suckers atrophied	DIASIA
Suckers not atrophied	PACHYTREMA

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A New Species of the Nematode Genus *Paraspidodera* from the Wild Pig.

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and Tropical Medicine.)

INTRODUCTION.

THIS description of a new species of *Paraspidodera* is based on material from the Helminthological collection of the London School of Hygiene and Tropical Medicine which was handed to the writer for examination by Professor R. T. Leiper, F.R.S. The parasite had been collected by Dr. Sells from the wild pig in Uganda ; no indication of the habitat is given. The writer wishes to thank Professor Leiper for placing this material at his disposal.

Paraspidodera sellsi n. sp.

The specimens were in a very poor state of preservation and the majority too badly macerated and contracted for detailed study. It was fortunate, however, that the material was abundant and, by examining a large number, a fairly complete description of the more important characters for identification can be given.

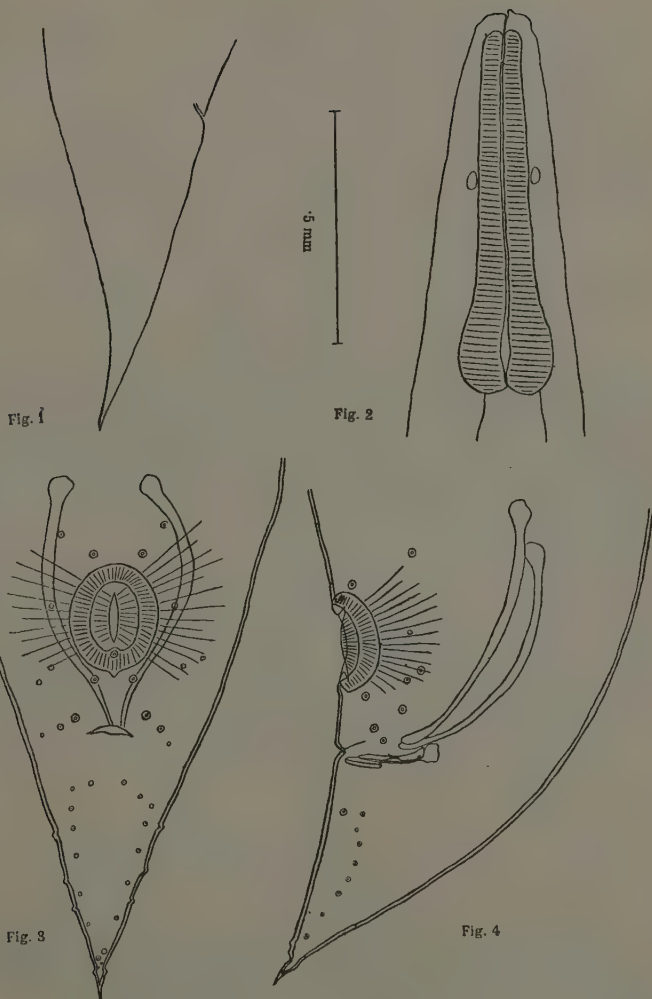
The mouth is surrounded by three lips which, although distinct, are not very strongly developed. The dorsal lip has a pair of short papillæ on its outer margin ; the two lateral lips have one papilla each on their outer margin and one fairly large finger-like papilla situated towards their inner side. This papilla is 0.01 mm. in length. The œsophagus measures from 0.66 mm. to 0.76 mm. in length and has a well marked posterior swelling without a constriction ; a valvular apparatus appears to be absent.

Owing to the state of the material further details concerning the characters of the head region and the presence or absence of a pharynx could not be made out with any certainty. Cervical alæ are absent and no cuticular markings have been observed.

Female.—The female has an average length of 17.5 mm., ranging from 15 mm. to about 20 mm., and a breadth of 1 mm. in the region of the vulva. The width at the head is 0.12 mm. Posteriorly the body narrows fairly sharply from the region of the anus and ends in a pointed tail, the distance from the anus to the posterior end being 0.72 mm. The vulva is a transverse slit a little in front of the middle of the body, 6 mm. to 7 mm. from the anterior end, and opens into a short vagina which turns posteriorly. The vagina is followed by a single uterine trunk which continues posteriorly for a distance of about 4 mm. from the vulva. At this point it divides into two branches, both of which turn anteriorly. The anterior branch continues forward well beyond the vulva while the posterior branch bends backward again before reaching the level of the vulva; at these points they become merged into coiled ovarian tubules.

Male.—The male is slightly shorter and narrower than the female, the average length being 15 mm. and the greatest width 0.75 mm. The posterior end is curved ventrally and narrows fairly rapidly from the anus, ending in a pointed tail measuring 0.55 mm. There is a preanal sucker present with a broad chitinous border situated about 0.25 mm. from the anus. The sucker is almost rounded, measuring 0.25 mm. in length and 0.2 mm. in breadth; a papilla-like process is present on the posterior margin. The two spicules are almost equal in length, slightly curved, and spatulate at the tip; the larger measures 0.58 mm. A gubernaculum is present and also a boat-shaped telamon measuring 0.18 mm. and 0.08 mm. in length respectively.

The poor condition of the material made the papillæ very difficult to observe and an examination of numerous specimens did not give a constant number. Their distribution however agrees fairly closely with that given for the related species *Paraspidodera uncinata*. Twenty-two pairs were observed, eight of which are preanal and one adanal. The remainder are postanal, and, with the exception of the two anterior pairs which are nearer the median line, they form two longitudinal lines towards the lateral margin of the worm when viewed ventrally.



Paraspidodera sellsi. Fig. 1, female tail. Fig. 2, head. Fig. 3, male tail, ventral view. Fig. 4, male tail, lateral view.

SYSTEMATIC POSITION.

This species, having an oesophagus with a posterior bulb and a preanal sucker with a chitinous rim, falls into the sub-family Heterakinae and appears to be related to *Paraspidodera uncinata* Travassos, 1914. It is possible, however, that an examination of fresh material would reveal sufficient differences, particularly in the character of the lips, to justify the erection of a new genus for *P. sellsi*. Travassos states that the lips in his species are "large like those of the genus *Ascaridia*"; in *P. sellsi* they do not appear to be so well developed. The other differences between the two species, namely in measurements and in the absence of a telamon in *P. uncinata*, together with the difference in host and locality, are only of specific importance. It should be noted that the above comparison is made with *P. uncinata* as described and figured by Travassos (1914) and not with *Subulura uncinata* (Rudolphi, 1819) Hall, 1916, with which Travassos considered his specimens to be identical. Hall, after comparing the descriptions and figures given by Travassos with those given by Schneider (1866) for Rudolphi's species, considered Travassos's species to be new, and he placed Rudolphi's species in the genus *Subulura*.

Although both these species are found in the same hosts, the writer agrees with Hall in his decision to keep them separate in view of the great difference between them in the shape and position of the preanal sucker. As Hall points out, this difference can hardly be accounted for by the fact that Schneider worked with poorly-preserved material, as a sucker with a chitinous rim would tend to remain distinct even in a macerated specimen. This was certainly the case in the specimens of *P. sellsi* examined by the writer.

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On *Acanthogyrus* n.g. from the Intestine of the Indian Fish *Labeo rohita*, with a Note on the Classification of the Acanthocephala.

By GOBIND SINGH THAPAR, M.Sc., Ph.D. (Lond.), F.R.M.S.

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OF the various groups of Helminths, Acanthocephala has received the least attention from Helminthologists; so much so that even its classification is based on very arbitrary characters. This may partly be due to the general belief that infestation with these worms is very rare. The earlier accounts, such as that of Diesing (1851), which deals with a number of species from fishes, giving brief descriptions of their external morphology and a few generalised drawings, describe the various species under a single genus, *Echinorhynchus*.

Hamann in 1892 described a few new genera, and divided the group into three families. But no published record includes a careful re-investigation on forms described by Diesing (1851), so that they have not yet been placed in their proper places in modern systems of classification.

Recently there has been a considerable addition to the number of the generic names. The results of the various investigations have, on several occasions, been summarised by Lühe (1911), Travassos (1917), Ward (1918), Van Cleave (1923) and Southwell and Macfie (1924), who have given, moreover, very useful keys for the identification of the known genera. Although these accounts form very useful and interesting additions to our knowledge of the Western forms, no data are available about the Asiatic species. The only available works on Asiatic Acanthocephala are those by Van Cleave (1918) and (1925) from China

and Japan respectively, and an account of a new species, *Centrorhynchus erraticus*, from Calcutta, by Chandler (1925). The present paper deals with an account of a new genus obtained in India from the intestines of the common rohu, *Labeo rohita*, and is named *Acanthogyrus acanthogyrus*. The form is interesting, as it shows not only affinities with several known genera, but apparently throws light on the general classification of the group. This has led me to suggest a tentative classification of the order.

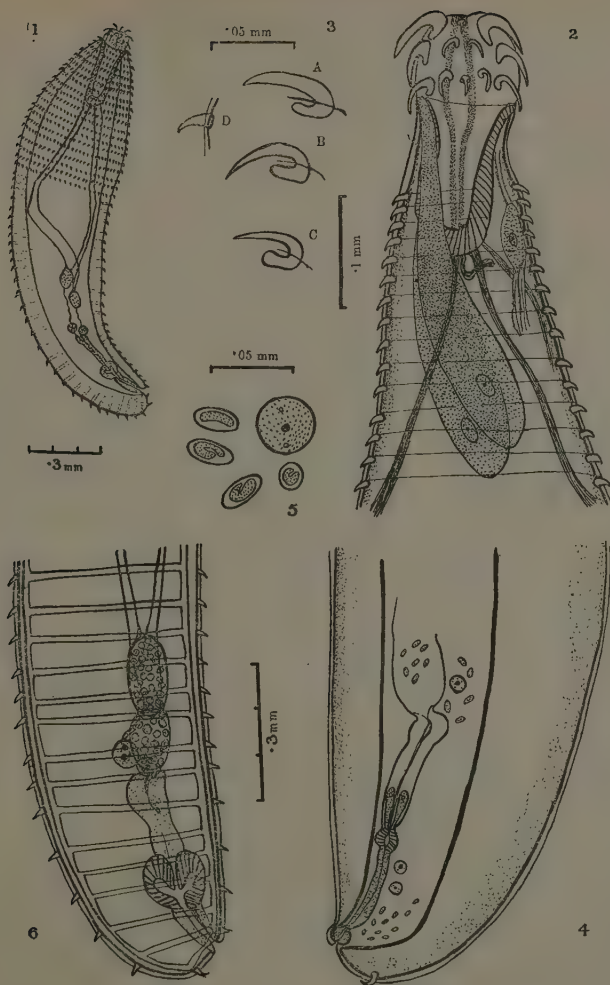
ACANTHOGYRUS ACANTHOGYRUS gen. et sp. nov.

The body is elongated club-shaped and is slightly swollen anteriorly behind the proboscis in both sexes. The male is smaller than the female and varies in length from 2 to 3 mm. with a maximum diameter of 0.45 to 0.55 mm. The female is about 6 mm. long by 0.9 mm. across its greatest width.

The proboscis is short, globular, and in most cases was found, after fixation, in a completely retracted condition within the body. The invertors of the proboscis and the retractors of the receptacle are strongly developed. In a fully expanded individual the proboscis is about 0.09 to 0.11 mm. long and bears three rows of eight recurved hooks deeply implanted in the proboscis wall. The relative lengths of the hooks in the three rows are as follows: anterior row, 60μ ; middle row, 50μ ; posterior row, 40μ . In all, the measurement of the root part of the hook is excluded; this is 20μ long. The exact shape and structure of the hooks of the various rows is shown in fig. 3. The proboscis sheath is thick walled and is about 0.13 mm. long.

The body is fairly stout and is covered with rose-thorn-shaped spines about 25μ long. The arrangement of the spines on the body varies in different regions. In the anterior part of the body there are 19 to 20 rows of spines completely encircling the body, but in the posterior part there is only a series of 20 to 21 paired spines laterally situated, representing the rings of the anterior part. The external characters thus indicate the presence of segmentation of the body.

This pseudo-segmentation has no correspondence in the internal anatomy, except in that of the lacunar system of the animal. Here we find a pair of lateral lacunar canals running along the entire length



ACANTHOGYRUS ACANTHOGYRUS.

- Fig. 1.—Male, general anatomy. Fig. 2.—Proboscis and anterior end of male.
 Fig. 3.—Proboscis hooks and body spines. (a), (b) and (c) proboscis hooks of the anterior, middle and posterior row respectively; (d) body spine.
 Fig. 4.—Posterior end of female, showing genitalia. Fig. 5.—Eggs from body cavity.
 Fig. 6.—Posterior end of male, showing genitalia and a part of the lacunar system.

of the body. These longitudinal lacunæ are connected by a large number of transversely running commissures, some of which anastomose with one another. The arrangement and distribution of a portion of the lacunar system is indicated in fig. 6. It is rather curious to find that the distribution of these commissures corresponds in position with the body spines. There are also two elongated pear-shaped lemnisci about 0.35 mm. long and projecting into the body cavity. They are longer than the proboscis sheath (receptacle).

The nerve ganglion is situated at 0.2 mm. from the anterior end of the body and lies at the base of the proboscis sheath.

The male has two ovoid testes situated in the posterior third of the body. They are lying one behind the other and are attached to the hinder end of the proboscis sheath by muscular ligaments. The anterior testis is a little larger than the posterior, their relative lengths being 0.17 mm. and 0.14 mm. respectively. Each has its own duct connecting it to its prostate gland. This relation is more clearly seen in specimens where the testes have not descended (fig. 1). Each prostate gland is a spherical structure containing two or more nuclei. The ductus ejaculatorius is peculiar in being Y-shaped, thus resembling the genus *Lueheia*, and it terminates in a large protrusible bursa. I have not been able to observe any trace of a penis. The genital aperture is guarded by curved spines which are a continuation of the series of the lateral body spines and are probably so modified for copulation.

The female genital system consists of an ovary, a large uterine bell, an elongated uterus, an ovejector and an elongated vagina. There are special flask-shaped gland cells lining the posterior part of the uterine wall. The genital opening here also is guarded by spines.

The eggs float about in the body cavity, into which they are discharged from the ovary. They are spherical, having a diameter of 40μ . The embryos are elliptical, 30μ by 15μ , and are enclosed within the egg-membranes. They are seen at various stages of development in the body cavity and the uterine bell.

The genus is of special interest because of the fact that it shows remarkable combinations of characters of several genera, like *Octospinifer*, *Corynosoma*, *Serrasentis*, *Lueheia* and *Quadrigyrus*, and probably indicates relationships with all. The chief characters on which the generic

diagnosis is based are as follows :—(1) three rows of eight recurved hooks on the proboscis ; (2) peculiar arrangement of the body spines ; (3) presentation of pseudo-segmentation ; (4) presence of only two prostate glands ; (5) Y-shaped ductus ejaculatorius.

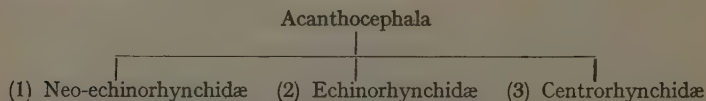
NOTE ON THE CLASSIFICATION OF ACANTHOCEPHALA.

Since the publication of the classical work of Hamann (1892), several attempts have been made to classify the group, but so far no satisfactory results have been obtained. Even the status of the group in the animal kingdom has been disputed. Rudolphi (1808) first gave it the status of a class under the phylum Nemathelminthes. Brumpt (1922) adopted a classification in which he makes Acanthocephala as an order. This has been accepted by Southwell and Macfie (1924), but recently Yorke and Maplestone (1926) revert to the designation of class. It will be well to adopt this status for Acanthocephala, as zoologists have abandoned the name "Vermes" as representing a phylum which includes all heterogeneous groups of worms with little or no inter-relationships. Taking Acanthocephala as a class, it should be divided into orders and families. In the ordinary course of events it would be desirable to raise the existing designations of the families to orders by a simple change in nomenclature ; but, unfortunately, there is no one classification that claims general confidence, and so this cannot be done.

The various classifications given by Travassos (1917), Ward (1918), Van Cleave (1923) and Southwell and Macfie (1924) fall under two main heads. One school follows Ward in basing their classification on "*the nature of the nuclei in the hypoderm and the lemnisci*." The other school of thought divides it on "*the nature of the prostate glands*." The latter view was propounded by Travassos (1917) and is upheld by Southwell and Macfie in their scheme. Both of these classifications are defective. Before discussing these systems fully it must be pointed out that every classification put forward must, in fairness to its author, be tested by the diagnosis which he gives. It must necessarily be based on a *natural system* and on features that are quite apparent and *constant*. Further, it must not relate to the minute details of a particular structure. Any classification that satisfies these points merits some consideration and subsequent acceptance.

Let us now discuss these two classifications with a view to judging their relative merits and see if we could accept any for general use.

Ward (1918) in giving his key to the families of North American Acanthocephala adopted the character of the nuclei in the hypoderm as the feature of first importance and divided the group into three families :—

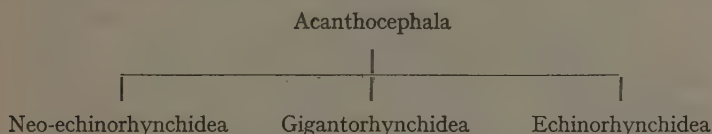


Of these families (1) and (2) are recognised on his basic character, but the family (3) is accepted on a different character altogether, *i.e.*, on the character of the attachment of the proboscis to the proboscis sheath. He places all three on the same level in his system and thus breaks down his own system by accepting a character other than the one proposed by himself.

However, the nature of the nuclei is not a character that could be relied upon for family diagnosis. In many instances, it is not an easy task to find out the exact nature and disposition of the nuclei in the hypoderm. Moreover, the genus *Quadrigyrus* Van Cleave, 1920, resembles the family Neo-echinorhynchidæ in general characters, except in that the nuclei in the hypoderm in the former are of two distinct types and in that its proboscis is armed with four rows of hooks. These characters necessitated the creation of a new family for the reception of this genus. The mere fact that several genera with more than three rows of hooks on the proboscis have been included in the family Neo-echinorhynchidæ incites that the difference from it of the family Quadrigyridæ is reduced only to the nature of the nuclei in the hypoderm. This seems to be attaching too great an importance to the minute details of a particular feature in structure. It is not desirable to consider it of such importance in our classification and should, therefore, be abandoned.

Travassos (1917) proposed his classification on the *nature of the prostate glands*, and Southwell and Macfie (1924), having both classifications at their disposal, selected this in preference to that of Ward (1918).

In accordance with this basis of classification, Southwell and Macfie have elaborated Travassos's system and added another feature to it in consideration of their family diagnosis. They have thus divided their order :—



These authors have further given the families of Travassos the status of sub-orders and have divided them into families, etc., thereby completely abandoning the nature of the nuclei in the hypoderm in their system of classification. The nature of the prostate may perhaps be zoologically sound but does not appear to be quite satisfactory as it is based on a sexual character which is, at times, very difficult to find. Even Southwell and Macfie have expressed doubts about the validity of considering this character of importance in classification of the group, and state: "*No reliance can be placed on the appearance of the prostatic glands of young worms. In mature worms it is frequently difficult to determine the number of prostatic glands, but as some authors attach great importance to it, we have been unable to avoid employing it as a diagnostic character. Moreover, our experience has convinced us that the shape and arrangement of the prostatic glands are by no means constant and as a diagnostic character must not be pressed too far; only differences of considerable degree are significant.*" The statement speaks for itself and shows the unsatisfactory nature of the character. It appears that they were unable to arrive at a more reliable solution and thus adopted this character in their scheme of classification. This character, besides being of a variable nature, seems to indicate an artificial basis for the system. No classification can be accepted, with present-day knowledge, as final, unless it is based on characters that are fairly representative of individuals, both male and female, and unless it is based on natural grounds.

The present genus, *Acanihogyrus*, presents characters in common with several genera that are isolated in different families in our arbitrary classifications. It combines characters of genera which appear to

possess natural affinities with one another and which, according to a natural system, ought to be grouped together under a common family or order. Under our present system, it is difficult to include the present genus under any known family, because of the characteristic features in its anatomy indicated in the text. To create a new family for a single genus, though tempting enough, would lead to a great multiplicity of families for single and isolated genera showing affinities with several known genera.

The writer, in the course of his study of the group, has considered various characters for the purpose of classification and has come to the following conclusion. He therefore presents a tentative classification, based on two characters, which seem to be fairly constant.

A review of the various genera of Acanthocephala shows that there are some genera that have only one root for the proboscis hooks, while in others the hooks have two distinct roots. Further, we find that in some cases, the body is armed with cuticular spines, while in others it is completely devoid of such structures. These two characters are fairly prominent and representative of individuals of both the sexes and thus form a natural basis of classification. Accordingly we can divide the class into three orders, two of which are further divided into families thus :—

- (2) APORORHYNCHIDEA nom. nov.—There are neither proboscis hooks nor body spines. It contains only one family, Apororhynchidæ, having one genus *Apororhynchus*.
- (2) ECHINORHYNCHIDEA.—Proboscis hooks only are present. There are no body spines. It contains several genera grouped under two families.
 - (a) ECHINORHYNCHIDÆ.—The proboscis hooks have only one root implanted in the proboscis wall.
 - (b) OLIGACANTHORHYNCHIDÆ.—The proboscis hooks have two distinct roots in the proboscis wall.
- (3) ACANTHOGYRIDEA nom. nov.—Proboscis hooks are present. The body is armed with cuticular spines. These body spines present different arrangements in different genera. This order also is divided into families.

- (a) *ACANTHOGYRIDÆ* fam. nov.—The proboscis hooks have only a single root.
- (b) *GIGANTORHYNCHIDÆ*.—The proboscis hooks have double roots in the proboscis wall. The proboscis is further characterised by the fact that it is non-retractile.

The new family *Acanthogyridæ* has been named after the genus described in the present communication in preference to other genera included under it. The writer considers *Acanthogyrus* to be a typical form from which other genera of the family could be derived by supposed modifications in the arrangement and the nature of the spines on the general body.

This classification is given in view of the fact that it indicates an adequate relationship of the different genera with one another within an order. It thus brings the class, *Acanthocephala*, in line with the other groups in the animal kingdom. A list of the recognised genera arranged under the proposed scheme of classification is as follows :—

Order 1.—*ECHINORHYNCHIDEA* Southwell and Macfie, 1924.

Family I.—*ECHINORHYNCHIDÆ* Cobbold, 1879.

Type.—*ECHINORHYNCHUS* Zœga, 1776.

Other genera.—*ACANTHOCEPHALUS* Koelreuter, 1771.

POMPHORHYNCHUS Monticelli, 1905.

OLIGOTERORHYNCHUS Monticelli, 1914.

MONILIFORMIS Travassos, 1915.

PROSTHORHYNCHUS Kostylev, 1916.

NEOECHINORHYNCHUS Stiles & Hassall, 1905.

TANAORHAMPIUS Ward, 1918.

GRACILISENTIS Van Cleave, 1919.

OCTOSPINIFER Van Cleave, 1919.

PANDOSENTIS Van Cleave, 1920.

LEPTORHYNCHOIDES Kostylev, 1924.

Family II.—*OLIGACANTHORHYNCHIDÆ* Southwell and Macfie, 1924.

Type.—*OLIGACANTHORHYNCHUS* Travassos, 1915.

Other genera.—*PROSTHENORCHIS* Travassos, 1915.

MACRACANTHORHYNCHUS Travassos, 1917.

Order 2.—ACANTHOGYRIDEA nom. nov.

Family I.—ACANTHOGYRIDÆ nom. nov.

Type.—ACANTHOGYRUS gen. nov.

Other genera.—CORYNOSOMA Lühe, 1904.

BOLBOSOMA Porta, 1908.

RHADINORHYNCHUS Lühe, 1911.

ARHYTHMORHYNCHUS Lühe, 1911.

CENTRORHYNCHUS Lühe, 1911.

POLYMORPHUS Lühe, 1911.

FILICOLLIS Lühe, 1911.

MEDIORHYNCHUS Van Cleave, 1916.

EMPODIUS Travassos, 1916.

TEGORHYNCHUS Van Cleave, 1920.

QUADRIGYRUS Van Cleave, 1920.

TELOSENTIS Van Cleave, 1923.

SERRASENTIS Van Cleave, 1923.

Family II.—GIGANTORHYNCHIDÆ Hamann, 1892.

Type.—GIGANTORHYNCHUS Hamann, 1892.

Order 3.—APORORHYNCHIDEA nom. nov.

Family.—APORORHYNCHIDÆ Shipley, 1900.

Type.—APORORHYNCHUS Shipley, 1900.

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A Survey of Welsh Helminthology.

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ALTHOUGH it was known that certain diseases of domestic animals in Wales were caused by parasitic worms, the systematic study of the economic importance of these worms did not begin until 1874, when Dr. Cobbold and a Mr. Rees Lloyd from Brecon investigated the "disastrous epizoöty" in the case of Welsh mountain ponies.

Cobbold (1879) stated that "Mr. Lloyd was the first to make search for helminths amongst some of the carcasses of the hundred and more equine animals that perished in South Wales," and "two distinct epizoötics prevailed. In the Beacons district tapeworms alone were the cause of death, whilst in the Deangunid district scores of animals perished from Strongyles. In another district a hundred animals perished from tapeworms." These worms were identified by Cobbold as examples of *Strongylus tetracanthus* and *Tænia perfoliata*.

This investigation of the epizoöty in horses of South Wales commenced in 1874, in which year Cobbold published some notes and articles in the *Veterinarian*, and also in the *Field*. A more complete account appears in the *Veterinarian* of 1875.

In 1875 Rees Lloyd quotes an instance of *Tænia serrata* from a dog in South Wales.

The earliest record of parasitic worms in relation to animal diseases in Wales was probably that found in the manuscripts of the old Welsh poet and historian Iolo Morganwg (Edward Williams, of Glamorgan). From 1790 to 1796 he made many itineraries through parts of Carmarthenshire, Pembrokeshire and Cardiganshire and studied the state of agriculture. In one of his manuscripts (deposited at the National Library of Wales, Aberystwyth) the following remedy is recommended for worms in sheep :—

“ As much sublimate as will lay on a shilling, in a quart of warm water, in which you may put a wine-glass of spirits of turpentine, answers completely.” Here is indicated the fact that worms caused trouble to sheep.

Iolo also remarked that “ rot ” (meaning “ liver-rot ”) occurred in the Kidweli marshes in Carmarthenshire, but it was not a common disease ; and that sturdy or gid (Bendro) occurred in cattle.

It is evident that at this period no investigations into the causes of the diseases of domestic animals had commenced, for Iolo Morganwg writes : “ State the propriety of proposing premiums for the best treatise on the causes and cures of diseases in cattle, horses, sheep and hog ; that these are useful animals and may be reared from the hands of murdering pretenders.”

In 1810 Walter Davies (otherwise known as Gwallter Mechain) declared the desirability of residents in Wales who “ should be scientific men who have studied the disorders of cattle.”

In his survey of South Wales, carried out in 1815, the same author recorded “ rot ” caused by the fluke-worm (*Fasciola hepatica*), and that “ the marsh pennywort, growing on poor wet soils, resembling the fluke-worm in roundness of form, is accused by peasants of causing rot, whence its name ‘ white-rot ’ ” ; and that “ a cough in calves, called in some parts whisk, is supposed to be caused by an insect, or its egg, taken from the tops of bent grasses in July or August.”

Apart from indirect evidence of the occurrence of helminthic parasites and the diseases caused by them, which is suggested in the publications of various Welsh druggists and veterinary quacks (particularly John Edwards of the Vale of Clwyd), no helminthological record appeared until that of Cobbold and Rees Lloyd in 1874.

After this another unfruitful period elapsed until the study of helminthology was taken up by research workers at the Welsh Colleges during the War, 1914 to 1918.

In 1917 C. L. Walton, working at Aberystwyth, recorded *Multiceps multiceps* and *Echinococcus veterinorum* from dog; *Distomum hepaticum*, *Moniezia spp.*, and *Strongylus filaria* from sheep; *Syngamus trachealis* from poultry; and *Ascaris suilla* from pig. In the same year the same author dealt with the problem of "liver-rot" in the sheep of North Cardiganshire, including Plynlymon, and also studied the bionomics of *Limnæa truncatula*.

Further information of the serious outbreak of "liver-rot" of the season 1920-21 (in Carnarvon, Denbigh, Anglesey and Flint) was given by C. L. Walton in his publication in 1922.

Unpublished observations of this serious outbreak were also made in the Aberystwyth area when the distribution of *Limnæa truncatula* in the Fairbourne district was mapped out in detail by J. R. W. Jenkins.

At this period (1922) came the report of an outbreak of trichinosis in human beings at Milford Haven, in Pembrokeshire. Thirteen cases occurred and it was ascertained that in each case they had eaten sausages procured from a particular butcher in the town, who had purchased pigs, or parts of pigs, from eight different farms in Pembrokeshire. The only other ingredient of the sausages was biscuit meal.

Flattely (1922) mentioned the *Moniezia* found in the Aberystwyth slaughterhouse.

In 1923 Jenkins, studying the genus *Moniezia*, created a new species, *Moniezia translucida*; and in 1924 he showed that the period of infection in lambs by *Moniezia spp.* was not confined to spring, but that it might extend at least until August: sheep as well as lambs were infected.

The examination of the intestinal contents of heavily infected lambs, the distribution of the genus *Moniezia*, and the fauna of infected farms gave no positive evidence as to the life-history of the tapeworms. J. R. W. Jenkins attempted to produce infection of possible intermediate hosts (*Arion ater*, *Agriolimax agrestis*, *Onthophagus nuchicornis*, *Aphodius fossor*, *A. fimetarius*, *A. merdarius*, *A. hæmorrhoidalis* and *Melophagus ovinus*) by feeding with mature proglottides, but with a negative result.

The following species have been recorded by him at Aberystwyth: *Moniezia alba* (Perroncito, 1879), *M. benedeni* (Moniez, 1879), *M. pellucida* (Blei, 1921), *M. translucida*, Jenkins, 1923, and *M. expansa* (Rudolphi, 1810).

C. L. Walton (1924) recorded *Anoplocephala perfoliata*, *Ascaris equi*, *Oxyuris equi* (*curvula*) and *Cylicostomum tetracanthum* from horses in North Wales. Also *Cænurus cerebialis* (occasional), *Echinococcus granulosus*, *Moniezia expansa*, *Fasciola hepatica* (common), *Dictyocaulus viviparus* (causing severe losses) and *Ascaris* sp. from cattle; *Fasciola hepatica*, *Moniezia planissima* (abundant), *M. expansa*, *M. alba*, *M. neumani*, *M. trigonophora*, *M. pellucida*, *Cysticercus tenuicollis* (fairly common), *Cænurus cerebialis* (fairly common) from sheep. The round worm *Hæmonchus contortus* is said to have caused serious trouble in the Vale of Clwyd; and *Æsophagostomum venulosum*, *Monodontus trigonocephalus*, *Nematodirus filicollis*, and *Trichuris ovis* were common parasites of sheep and widely distributed. *Dictyocaulus filaria* has been reported as causing death in sheep. From pigs he obtained *Fasciola hepatica* and *Ascaris lumbricoides* (abundant); from rabbits *Fasciola hepatica*, *Cysticercus pisiformis*, *Echinococcus granulosus* (the "large cysts" which Walton mentions in connection with this are possibly those of *Cænurus serialis*.—E. A. L.), and from poultry *Raillietina echinobothrida* (causing death of several fowls in Anglesey in 1923), *Hymenolepis lanceolata* (from goose), *Davainea cesticillus* (once from Radnorshire), *Heterakis vesicularis*, and *Syngamus trachealis* (causing occasional losses).

The work carried out by Walton covered a wide area. The step which naturally followed was the carrying out of intensive, and thus more detailed, surveys of smaller areas.

Such work was made possible by the Institute of Agricultural Parasitology, London School of Hygiene and Tropical Medicine, for in 1923 D. O. Morgan, working under the direction of Prof. R. T. Leiper, began his intensive survey of the parasitic helminths of domestic animals in the Aberystwyth area. In 1924 Morgan published the result of the survey for the first six months (October, 1923, to March, 1924), and made the following new records for the Aberystwyth area.

From eighty sheep he obtained *Cysticercus tenuicollis* (common), *Monodontus trigonocephalus* (very common), *Æsophagostomum venulosum*, *Chabertia ovina*, *Trichuris ovis* (common), *Capillaria longipes* (rare),

Hæmonchus contortus (three times), *Nematodirus filicollis* (abundant in October and November), *Cooperia curticei* (common, but not abundant), *C. onchophora* (once), *Ostertagia circumcincta* (frequent), *Trichostrongylus vitrinus* (few times); from twenty-five cattle *Fasciola hepatica* (few occasions), *Moniezia spp.* (twice), *Monodontus phlebotomus* (three occasions)—this being the first record of this parasite from cattle in Great Britain). *Æsophagostomum radiatum*, *Chabertia ovina* (few times), and *Cooperia onchophora* (two occasions); from seventeen pigs, *Cysticercus tenuicollis* (generally frequent, heavy in March), *Æsophagostomum dentatum* (abundant on two occasions), *Metastrongylus elongatus* and *M. brevivaginatus* (very common) and *Trichuris suis* (common).

In 1925 D. O. Morgan published the result of his survey for March, 1924, to September, 1924. He made the additional new records of *Dictyocaulus filaria* (frequent in lambs in summer), *Ostertagia trifurcata* (scarce) and *Strongyloides papillosus* (scarce) from lambs. He also found that though lambs harboured a large number of intestinal parasites they were in good condition to be slaughtered for food; there was a marked difference in the number and in the species of helminths found in lambs and sheep; the age of the host was an important factor in the helminthic infection; while *Moniezia spp.* was most common in May, there was a distinct drop in the percentage in midsummer, with a rise again in August and September, with a gradual disappearance of the parasite as the lambs became older; the age of the host was a factor determining the presence or absence of *Monodontus trigonocephalus*; No *M. trigonocephalus* were found in lambs during April and May, but adult worms appeared towards the end of June, and older sheep were abundantly infected throughout the year.

It was at this time (1925) that Norman Bissett, Veterinary Adviser at Cardiff College, published in the *Welsh Journal of Agriculture* an article in which he recorded *Anoplocephala mamillana*, *Cylicostomum tetracanthum*, *Strongylus edentatus*, *S. vulgaris*, *S. equinus* and *Oxyuris* from horses in South Wales.

In October, 1925, the writer succeeded Morgan as Field Officer at Aberystwyth, and in the same year published a paper in which he shewed that *Syngamus trachea* occurred in the rook, thrush, jay and starling, the last-mentioned bird being infected to the extent of 37 per cent.

Owing to their various migrations in large flocks the starlings were considered to be important factors in the distribution of the parasite and consequently of the "gapes" disease in poultry.

A further paper dealing with starlings and the "gapes" disease showed that out of 482 starlings examined, 35 per cent. were infected.

In 1926 the writer recorded a number of helminths collected from wild birds; and also published some observations on the incidence of *Metastrongyles* in the pigs of Central Wales.

In the same year (1926) further contributions to the knowledge of parasitic worms in animals occurring in Wales were made by Norman Jones, of Bangor, and Dilwyn John, of Aberystwyth. The former carried out a survey of helminths occurring in domestic animals slaughtered in various centres of Anglesey, Pwllheli, Carnarvon, Bangor, Conway and Llandudno. The species recorded were the same as those previously found at Aberystwyth by Morgan and the conclusions reached as a result of the survey were somewhat similar.

Dilwyn John described the anatomy and histology of a tapeworm *Cittotænia denticulata* (Rudolphi, 1804) found in the rabbits of the Aberystwyth area. He also recorded *Cysticercus pisiformis*, *Cœnurus serialis*, *Graphidium strigosum*, and *Trichostrongylus retortæformis*: and attempted to elucidate the life-histories of *Cittotænia denticulata* and *C. pectinata* (Goeze, 1782), but his efforts were not attended with success. Experiments by feeding the following insects with *Cittotænia* eggs were carried out by this author: *Aphodius punctatosulcatus*, *A. fimetarius*, *Oxytelus sculpturatus*, *Oleochara lanuginosa*, *Gercyon melanocephalus*, *Sphaeridium quadrimaculatum*; the mite *Pergamasus crassipes*, var. *longicornis*, and the rabbit flea, *Spilopsyllus cuniculi*, were also used.

In 1927 the writer published a list of parasitic helminths found in horses examined at Aberystwyth, and Norman Bissett made observations on verminous broncho-pneumonia in the pig, caused by *Metastrongyles*. The latter author described cases of death caused by these lung-worms and stated that "chloroform administered intra-nasally in doses of 2 c.c. per pig—1 c.c. per nostril—by means of a double nozzled hypodermic syringe appears to be effective" in curing the disease. Some few experiments carried out with the larval forms of *Metastrongyles* showed that the free larva could withstand a temperature six degrees below freezing-point.

R. F. Montgomerie (1925-27) cited instances of rapid loss in condition, and death, of many sheep in North Wales due to an outbreak of alimentary helminthiasis. The parasites found in one case examined were *Hæmonchus contortus*, *Trichuris ovis*, and *Æsophagostomum venulosum*. Carbon tetrachloride and extract of male fern as anthelmintics in the treatment for liver-rot and alimentary infestations by helminths were dealt with by Mr. Montgomerie in various publications.

Rees Wright (1927) redescribed the redia and cercaria of *Fasciola hepatica*, and made observations which suggest that *Limnæa peregra* also may act as an intermediate host to *F. hepatica*. Two apparently new cercariæ, from *L. truncatula*, are also described by him.

The following is a list of the Trematoda, Cestoda and Nematoda collected by the writer in the Aberystwyth area:—

TREMATODA.

Parasite.	Position in Host.	Main Host.
<i>Echinostomum paraulum</i> Dietz, 1909	Rectum	Whooper swan.
" <i>revolutum</i> (Frölich, 1802)	Small intestine and rectum	" "
<i>Himasthla elongata</i> (Mehlis, 1831) ...	Small intestine ...	Herring gull.
<i>Echinochasmus coarctatus</i> , Dietz, 1909	" " ...	Bittern.
<i>Paryphostomum radiatum</i> (Duj., 1845)	" " ...	Cormorant.
<i>Petasiser exaratus</i> , Dietz, 1909 ...	Stomach and small intestine	"
<i>Parorchis acanthus</i> , Nicholl, 1907 ...	Small intestine ...	Herring gull.
<i>Opisthioglyphe rana</i> (Frölich, 1802) ...	" " ...	Common frog.
" <i>hystrix</i> (Molin, 1861)...	" " ...	" "
<i>Pneumonæces variegatus</i> (Rud., 1809)...	Lung	" "
<i>Haplometra cylindracea</i> (Zed., 1800) ...	Lung and mouth ...	" "
<i>Omphalometra flexuosa</i> (Rud., 1802) ...	Small intestine ...	Mole.
<i>Lepoderma cirratum</i> (Rud., 1802) ...	" " ...	Blackbird.
<i>Lyperosomum longicauda</i> (Rud., 1809)	Liver	"
<i>Ityogonimus ocreatus</i> (Goeze, 1787) ...	Small intestine ...	Mole.
" <i>filum</i> Looss, 1907 ...	" " ...	"
<i>Galactosomum lacteum</i> (Jägerskiöld, 1896)	" " ...	Cormorant.
<i>Spelotrema simile</i> Jägerskiöld, 1900 ...	" " ...	Herring gull.
<i>Cryptocotyle concava</i> (Creplin, 1825)	" " ...	" "
" <i>lingua</i> (Creplin, 1825) ...	" " ...	" "
<i>Catatropis verrucosa</i> (Frölich, 1789) ...	Cæcum	Whooper swan.
<i>Strigea longicollis</i> (Rud., 1819) ...	Small intestine ...	Cormorant.
<i>Strigea variegata</i> (Creplin, 1825) ...	Small intestine ...	Cormorant.
<i>Polystomum integerrimum</i> (Frölich, 1802)	Urinary bladder ...	Common frog.

CESTODA.

Parasite.	Position in Host.	Main Host.
<i>Anoplocephala perfoliata</i> (Goeze, 1782)	Intestine and Cæcum	Horse.
<i>Dipylidium caninum</i> (Linnaeus, 1758)	Small intestine ...	Dog.
" <i>sexcoronatum</i> Ratz, 1900	" " ...	" "
<i>Dipylidium</i> spp.	" " ...	Dog and cat.
<i>Echinocotyle vosseteri</i> , Blanchard, 1891	" " ...	Domestic duck.
<i>Hymenolepis diminuta</i> (Rud., 1819) ...	" " ...	Brown rat.
" <i>nana</i> (Siebold, 1852) ...	" " ...	" "
<i>Hymenolepis</i> sp.	" " ...	Mole.
<i>Echinococcus granulosus</i> (Batsch, 1786)	" " ...	Dog.
<i>Multiceps multiceps</i> (Leske, 1780) ...	" " ...	"
" <i>serialis</i> (Gervais, 1847) ...	" " ...	"
<i>Tænia hydatigena</i> (Pallas, 1766) ...	" " ...	Dog and cat.
" <i>pisiformis</i> (Bloch, 1780) ...	" " ...	" "
" <i>taniaformis</i> (Batsch, 1876) ...	" " ...	" "
" sp.	" " ...	Mole.

NEMATODA.

Parasite.	Position in Host.	Main Host.
<i>Ascaris equorum</i> , Goeze, 1782	Intestine	Horse.
" <i>ovis</i> , Rud., 1819 '	"	Sheep.
<i>Toxocara canis</i> (Werner, 1782)	"	Dog.
" <i>mystax</i> (Zeder, 1800)	"	Cat.
<i>Ascaridia columba</i> (Geml., 1790)	"	Pigeon.
" <i>perspicillum</i> (Rud., 1803)	"	Domestic fowl.
<i>Porrocaecum crassum</i> (Deslongchamps, 1824)	"	" duck.
" <i>depressum</i> (Zed., 1800)	Small intestine ...	Hooded crow.
" <i>ensicaudatum</i> (Zed., 1800)	" " ...	Starling, blackbird, rook.
" <i>semiteres</i> (Zed., 1800)	" " ...	Rook, starling.
" <i>spirale</i> (Rud., 1795)	" " ...	Barn owl.
<i>Contracaecum spiculigerum</i> (Rud., 1809)	Stomach	Cormorant.
<i>Oxyuris equi</i> (Schränk, 1788)	Intestine	Horse.
<i>Cosmocerca ornata</i> (Duj., 1845)	Small intestine ...	Common frog.
<i>Aplectana brevicaudata</i> (Zed., 1800) ...	" " ...	" "
<i>Heterakis vesicularis</i> (Frölich, 1791) ...	Cæcum	Domestic fowl.
" <i>brevispiculum</i> Gendré, 1911 ...	"	Guinea-hen.
" <i>dispar</i> (Schränk, 1790)	"	Goose.
" <i>spumosa</i> (Schneider, 1866)	"	Brown rat.
<i>Subulura suctoria</i> (Rud., 1819)	"	Night-jar.
" <i>andersoni</i> (Cobbold, 1876)	"	Squirrel.

Parasite.	Position in Host.	Main Host.
<i>Strongylus</i> (<i>Strongylus</i>) <i>equinus</i> (Mueller, 1780 <i>ex parte</i>)	Right ventral colon	Horse.
<i>Strongylus</i> (<i>Alfortia</i>) <i>edentatus</i> (Looss, 1900)	" " "	"
<i>Strongylus</i> (<i>Delafondia</i>) <i>vulgaris</i> (Looss, 1900)	Cæcum ...	"
<i>Æsophagodontus robustus</i> (Giles, 1892)	Right ventral colon	"
<i>Craterostomum mucronatum</i> (Ihle, 1920)	Dorsal colon ...	"
<i>Trichonema</i> (<i>Trichonema</i>) <i>ægyptiacum</i> Le Roux, 1924	Intestine ...	"
<i>Trichonema</i> (<i>Trichonema</i>) <i>coronatum</i> (Looss, 1900)	" ...	"
<i>Trichonema</i> (<i>Cylicostephanus</i>) <i>calicatum</i> (Looss, 1900)	Cæcum ...	"
<i>Trichonema</i> (<i>Cylicostephanus</i>) <i>longibursatum</i> (Yorke and Macfie, 1918)	Large colon and cæcum	"
<i>Trichonema</i> (<i>Cylicostephanus</i>) <i>minutum</i> (Yorke and Macfie, 1918)	Intestine ...	"
<i>Trichonema</i> (<i>Cylicocercus</i>) <i>goldi</i> (Boulenger, 1917)	Ventral colon and cæcum	"
<i>Trichonema</i> (<i>Cylicocercus</i>) <i>pateratum</i> (Yorke and Macfie, 1919)	Cæcum ...	"
<i>Trichonema</i> (<i>Cylicocercus</i>) <i>alveatum</i> (Looss, 1900)	Ventral colon ...	"
<i>Trichonema</i> (<i>Cylicocyclus</i>) <i>nassatum</i> (Looss, 1900)	" " ...	"
<i>Trichonema</i> (<i>Cylicocyclus</i>) <i>insigne</i> (Boulenger, 1917)	Right dorsal colon...	"
<i>Trichonema</i> (<i>Cylicocyclus</i>) <i>elongatum</i> (Looss, 1900)	Cæcum ...	"
<i>Trichonema</i> (<i>Cylicocyclus</i>) <i>radiatum</i> (Looss, 1900)	" ...	"
<i>Triodontophorus serratus</i> (Looss, 1900)	Large colon ...	"
" <i>brevicauda</i> , Boulenger, 1916	Cæcum ...	"
<i>Uncinaria stenocephala</i> (Railliet, 1884)	Small intestine ...	"
<i>Oswaldocruzia bialata</i> (Molin, 1861) ...	" " ...	Common frog.
<i>Ollulanus tricuspis</i> , Leuckart, 1865 ...	Stomach wall ...	Cat.
<i>Syngamus trachea</i> (Montagu, 1811) ...	Windpipe ...	Starling, chicken, thrushes, jay, pheasant.
<i>Dictyocaulus filaria</i> (Rud., 1809) ...	Bronchiole ...	Sheep.
<i>Crenosoma striatum</i> (Zed., 1800) ...	Bronchi ...	Hedgehog.
<i>Protostrongylus rufescens</i> (Leuckart, 1865)	Lung ...	Sheep.
<i>Æleurostrongylus abstrusus</i> (Railliet, 1898)	" ...	Cat.
<i>Muellerius capillaris</i> (Mueller, 1889) ...	" ...	Sheep.
<i>Rhabdias bufonis</i> (Schränk, 1788) ...	Lung and mouth ...	Common frog.

<i>Parasite.</i>	<i>Position in Host.</i>	<i>Main Host.</i>
<i>Capillaria anatis</i> (Schränk, 1790) ...	Small intestine ...	Domestic duck.
" <i>annulosa</i> (Duj., 1845) ...	" " ...	Brown rat.
" <i>erinacei</i> (Rud., 1819) ...	" " ...	Hedgehog.
" <i>linstowi</i> Trav., 1914 ...	Urinary bladder ...	Mole.
" <i>linearis</i> (Leidy, 1856) ...	" " ...	Cat.
" <i>ovopunctata</i> (Linst., 1873) ...	Small intestine ...	Starling.
" <i>tenuissima</i> (Rud., 1803) ...	" " ...	Barn owl.
<i>Trichosomoides crassicauda</i> (Bellingham, 1840)	Urinary bladder ...	Brown rat.

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On the Nomenclature of the Vinegar Eelworm.

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INTRODUCTION.

THIS eelworm, only just visible to the naked eye, and quite common in vinegar in all parts of the world, has long been known to zoologists, and indeed was an object of keen interest and discussion to the naturalists of the seventeenth century. Petrus Borellus [3], for instance, enthusiastic over the recent adoption of the microscope for researches in natural history, published in 1656 his "Observationum Microscopiarum Centuria," in which he leads off with a note "De Vermibus aceti." In the twelfth edition of the "Systema Naturæ" (1767), Linnæus [10] included a species *redivivum* in that final genus of the Regnum Animale so appropriately named *Chaos*. This species of animal he says, "Habitat in Aceto & Glutine Bibliopegorum."

Some of the earliest recorded biological experiments were concerned with the vinegar eel, notably those described in the long paper by Goeze of Quedlinburg [7], with which the first volume of "Der Naturforscher" opened, in 1774. Goeze considered that the worms in vinegar and those in bookbinders' paste were distinct forms. Subsequent authors fell into conflicting camps over this question: some emphatically denied the identity of the two forms, while others asserted it with equal emphasis. The question remained undecided until quite recent years: in 1910 de Man [11] published a detailed account of the anatomy of the vinegar eel, and in 1922 Goodey [8], while doing the same for the paste eel, showed beyond question that the species were distinct, the most pronounced differences lying in the shape of the spicules and of the accessory piece.

The nomenclature of these two worms presents a confused problem

which has been complicated still further by the question of their identity mentioned above. This study represents an attempt to set forth the difficulties, and to point out some apparent misconceptions, surrounding the nomenclature of the vinegar eelworm, but it will be clear from what precedes that the paste eelworm is also implicated. Finally, a possible solution of the difficulties is suggested.

I am indebted to Professor R. T. Leiper for helpful advice, and more specifically for the loan of several old monographs relevant to the problem. Many of the latter are almost inaccessible outside of the National Library.

It will be convenient to deal with the development of the problem in two periods, the first comprising the work of Linnæus and O. F. Müller (*i.e.*, up to 1786), and the second that of Hemprich and Ehrenberg (1828) and subsequent authors.

First Period (1767-1786).

It has been pointed out that Linnæus [10] in 1767 proposed the name *Chaos redivivum* for certain worms "in Aceto & Glutine Bibliopegorum," and there can be little doubt that these were the vinegar and paste eels considered as a single species. The specific diagnosis is rather vague from a modern point of view ("filiforme utrinque attenuatum"), but considered in conjunction with the habitat and the references (Baker, Needham, Ledermüller) it may be accepted as adequate.

In 1773, O. F. Müller [12] published his "*Vermium Terrestrium et Fluviatilium*," containing a genus *Vibrio* which comprises a very heterogeneous collection of animals. One species of the genus, *V. anguillula*, is to be found "in glutine farinoso & alibi vulgatissimum." Müller gives the common Danish name, "Aal-straekkeren," and definitely refers back to *Chaos redivivum* as a synonym. It may be pointed out at once that, according to the procedure of modern nomenclature, the new specific name is quite unjustified: in placing *redivivum* into a new genus, the old specific name should stand, and *Vibrio anguillula* should become *Vibrio redivivus*. (*Vibrio* appears to have been used as a masculine noun, substantival specific names—like *anguillula*—remaining unchanged.)

In the "*Zoologiæ Danicæ Prodromus*" of 1776, Müller [13] repeats the name *Vibrio anguillula* and the reference to Linnæus. He later (1783) refers to an addendum to this work, but I was unable to find it in the copy I saw (National Library).

In 1783 he published a Review [14] of some of the articles appearing in the ten first volumes of "Der Naturforscher." Here he refers to Goeze's contribution, where the latter speaks of the vinegar and paste eels as distinct forms. Müller agrees, and mentions the addendum to his own work of 1776. From this he quotes the following: "*Anguillulæ aceti, glutinis farinosi, aquæ dulcis et aquæ marinæ specie differunt . . .*" I wish to suggest that he is not here speaking nomenclatorially (*i.e.*, *anguillula* is not here raised to generic rank), but intends to say merely that these four eelworms differ in appearance: thus he does not employ the usual single word of a specific name, but extended descriptive phrases. This is borne out by a table which immediately follows in the Review (p. 162), and which is so vital to the present problem that it may be quoted in all its essentials:

Vibrio fluvialis; Süßwasserälchen.

Vibrio Anguillula, Verm., 1, 41 [*i.e.*, Müller, 1773].

Anguille vulgaire, ROZIER, etc.

V. aceti; Essigälchen.

Anguille du vinaigre, ROZIER, etc.

V. glutinis. Kleisterälchen.

Vibrio anguillula. Verm., 1, 41 [*i.e.*, Müller, 1773].

Chaos redivivus filiforme utrinque attenuatum. Linn. *Syst.*, 1326.

Anguille de la colle, ROZIER, etc.

V. marinus. Meerwasserälchen.

It will be noticed that the former species *anguillula*, 1773, is here divided into *fluvialis* and *glutinis*, and that *aceti* and *marinus* are added—all under the genus *Vibrio*. The vinegar eel is not regarded as having been included in the former *V. anguillula*, and the paste eel is definitely identified with *Chaos redivivum*. It is necessary to note that the above list is not intended to exhaust the genus *Vibrio*: both in earlier (1773, 1776) and in later (1786) works Müller gives a much more extensive list of species. Applying modern procedure to this stage, it is seen that *Vibrio glutinis* Müller, 1783, equals *Vibrio anguillula* Müller, 1773, in part, and to the species *glutinis*, 1783, is confined *Chaos redivivum* Linnæus, 1767. Stiles and Hassall [21] have recorded views similar to the above; on page 35 of their "Determination of Generic Types" they say: "From the facts thus far given it is clear that *glutinis*, 1783, is the lineal descendant of *anguillula*, 1773, seu *redivivum*, 1767."

In his next relevant publication, however, Müller (1786) [15] retracts the above classification, and reverts to *Vibrio anguillula*, with *aceti*, *glutinis*, *fluviatilis* and *marina* as varieties within the species. It is important that this statement should be substantiated, for Stiles and Hassall have based an argument, making *redivivum* type of the genus *Anguillula* Müller, 1786, on the assumption that Müller here raised the name *anguillula* to generic rank, with *aceti*, *glutinis*, etc., as species. They say (*loc. cit.*): "The next work of importance is Müller, 1786, 63 (*Animalcula Infusoria*), which is not accessible to us. According to Gmelin (1790A, 3900-3901) and Sherborn (1902, 1077), *Anguillula* was proposed by Mueller, 1786, 63, with four species, . . ." Careful examination of Müller's 1786 publication discourages agreement with Gmelin and Sherborn. At the beginning of the work Müller gives a list of genera (pp. xxvi and xxvii) which includes *Vibrio* but does not include *Anguillula*. There follows (pp. xxviii-lvi) a list called "Denominaciones Specificæ" which includes amongst others all the species of *Vibrio*. Number 15 of this genus reads simply: "*Anguillula, æqualis, subrigidus*"; there is even no mention here of the four varieties. On page 63, where the description of *anguillula* commences, the name and brief diagnosis just quoted are repeated, and the heading, "*Vibrio Anguillula*," is in every way comparable with that of other species throughout the book. Then follow four sub-headings introduced by the letters α , β , γ , δ , and consisting of the names *Anguillula aceti*, *Anguillula glutinis*, etc. Nowhere else in the work was this form of subdivision (introduced by Greek letters) seen. Finally, after describing *aceti* and *glutinis*, Müller adds a note: "*Hæ duæ varietates nimis affines*"; and speaking of the whole species he says: "*Hujus quatuor saltem varietates, si non distinctæ species, dantur, nempe Anguillula aceti, glutinis farinosi, aquæ dulcis & aquæ marinæ, quæ revera differunt, . . .*" (*italics original*). Thus it is clear that he thinks they may be distinct species, but (and surely this is the point of forensic importance) it is equally obvious that he treats them *formally* as varieties. This question, of the formal status of the names *aceti*, etc., has been dealt with at great length because Stiles and Hassall appear to have been misled by Gmelin and by Sherborn; and the former authors have based a ruling on this misconstrued status. It will be convenient to deal here with the argument of Stiles and Hassall.

First it may be noted that *Anguillula aceti* and *A. glutinis* (or *rediviva*)

are the names which have been employed fairly consistently in recent years for the vinegar and paste eels respectively, some authors deriving *Anguillula* from Müller, 1786, and others from Hemprich and Ehrenberg, 1828 (*vide infra*, "Second Period"). Stiles and Hassall follow the first group. Further, on the assumption that Müller (1796) raised *anguillula* to generic rank, they argue that *rediviva* (= *glutinis*) is type by tautonymy of this genus. In their own concise words, "In *Anguillula* Müller, 1796 there is a species *glutinis*, 1783, with *anguillula*, 1773, as synonym; hence *anguillula*, 1773, is type by tautonymy of *Anguillula* 1796, but as *anguillula*, 1773, equals *redivivum*, 1767, renamed this latter name in its emended sense—namely, as equal to *glutinis*, 1783—should stand as type species of *Anguillula*, 1786. The correct name for the 'Kreisteraelchen' is thus seen to be *Anguillula rediviva* (Linnaeus, 1767; Stiles and Hassall, 1905." If it is accepted that *anguillula* 1796 is merely a specific name, then the argument for "type by tautonymy" breaks down. Moreover, so far as we have considered, there is no available genus for *aceti* and *redivivum* unless it be Müller's *Vibrio* or Linnaeus' original genus *Chaos*.

Stiles and Hassall '21, (*op. cit.*, pp. 32 and 43) have shown good reason for regarding *Chaos* as a genus of *Proterozoa* with *Chaos chaos* (Linnaeus, 1758) Stiles, 1905 (= *Amoeba proteus*), as type. And with reference to the genus *Vibrio* they say: "This case is so complicated that we have no desire to suggest a ruling upon it at present." So far as we have followed it, however, the nomenclature seems to be emancipated from any further necessity of consideration as type of *Vibrio*."

Thus, from a study of the literature up to 1786, it is concluded that the species *aceti* and *redivivum* are left without a valid genus.

Second Period (1828-1922).

After the publication of Müller's "Animalcula Infusoria" in 1786, the next relevant work is the "Synopsis Physica" of Hemprich and Ehrenberg, 1828. In this work is a new genus, *Anguillula*, containing Müller's *Vibrio anguillula* formicae, 1786, Müller's *Vibrio coluber*, 1786, and three new species. Its type is here designated, but Stiles and Hassall have unfortunately designated *formicae* = *formicilis*, by "page precedence, elimination and other factors." In addition, it is interesting to note that Hemprich, 1828, is a listed synonym of *Vibrio anguillula*, 1773.)

In 1838, Ehrenberg [6] included *aceti* and *glutinis* in the genus *Anguillula*, 1828; and in 1865, Bastian [1] designated *aceti* as type of this genus. Baylis and Daubney [2] (1926)—who reject *Anguillula* Müller, 1786, on the grounds already mentioned—accept Bastian's designation of *aceti* as type of "*Anguillula* Ehrenberg, 1831" (? Hemprich and Ehrenberg, 1828), since it is an easily recognised species, while "The original diagnosis of this genus given by Ehrenberg (1831) is valueless from the modern standpoint, as is that of the probable genotype, *A. fluviatilis*," and further, "*fluviatilis* and the other species recognized by Ehrenberg in 1831 are probably unrecognizable" (p. 39). But, as Stiles and Hassall point out, neither *aceti* nor *redivivum* was included in the original genus (1828), so that *aceti* "could not under any circumstances be type of '*Anguillula* Ehrenberg'" (*op cit.*, p. 37; see also "Règles internationales de la Nomenclature zoologique adoptées par les Congrès internationaux de Zoologie," 1914 [16], Article 30, II, e), α). Thus it would seem that *Anguillula*, 1828, was quite valid (*i.e.*, was not preoccupied by a supposed *Anguillula* Müller, 1786), but that the genotype and other original species are probably not recognizable, in which case the genus is a nomen nudum. Even if the genotype is recognizable, it is very unlikely that it is congeneric with *aceti* and *redivivum*. (Bastian [1] says: "The few definite characters given . . . seem pretty positively to indicate that this species *fluviatilis* does not in reality belong to the genus *Anguillula*. Any free nematodes . . . which have been accidentally met with . . . hitherto, have been provided with the convenient name of *Anguillula fluviatilis*; . . . It may perhaps belong to the genus *Plectus*," p. 113.) Moreover, it may be added that one of the original generic characters, that of the single spicule ("penis marium simplex"), would in any case exclude *aceti* and *redivivum*. It would therefore seem very doubtful whether the two latter species can be allowed to remain in *Anguillula* Hemprich and Ehrenberg, 1828.

So far, then, *aceti* and *redivivum* are barred from *Chaos* and *Vibrio*, and almost certainly from *Anguillula*, 1828; and *Anguillula*, 1786, does not exist. There remain to be considered certain other genera into which the two species have been placed.

In 1815, Oken [17] placed *aceti* and *glutinis* (= *redivivum*) into the genus *Gordius* Linnæus, 1758. According to Stiles and Hassall (*op. cit.*, pp. 64 and 109) this arrangement cannot stand, for they make *aquaticus*

type (by Linnæan rule) of the genus, and the latter is not congeneric with the former species.

Dujardin (1845) [5] removed *aceti* and *glutinis* from *Anguillula*, 1828, and placed them in his genus *Rhabditis*, 1845. Of this genus, Bastian [1] designated *terricola* as type. Stiles and Hassall have suggested that *glutinis* might be considered type by inclusion (as type of the supposed earlier genus *Anguillula* Müller, 1786): this alternative is now vitiated, thus avoiding what would have been an unfortunate revolution in accepted nomenclature. Bastian's designation of *terricola* can therefore stand, and *aceti* and *redivivum* must be removed. (The absence in the two latter of the typical pharyngeal rods and of the male caudal alæ, may be cited as important differences.)

Diesing [4] (1851; *vide* Stiles and Hassall) returned *aceti* and *glutinis* to *Anguillula*.

Schneider (1866) [18] placed *aceti* and *glutinis* in the genus *Leptodera* Dujardin, 1845 (= *Leptoderes* Dujardin, 1845), and united them in the single species *oxophila* (*oxyphila* Minot, *vide* Stiles and Hassall). There is no warrant for the new specific name, and the species are now known to be distinct. This genus is monotypic (*flexilis*, 1845), and the long conical œsophagus and male caudal alæ of the type differentiate it clearly from the vinegar and paste eels: the latter therefore cannot remain in *Leptodera*.

In his important paper of 1910, de Man retains "*Anguillula* Ehrenberg" and defines it on the basis of *aceti*. He also describes *Rhabditis dryophila* Leuckart, considering it a variety of *Anguillula aceti*, and describes a new species, *Anguillula ludwigii*.

Goodey (1922) reviews the systematic position, and accepts the argument of Stiles and Hassall, making *Anguillula rediviva* (Linnæus, 1767) Stiles and Hassall, 1905, type of the supposed genus *Anguillula* Müller, 1786.

The foregoing account of the nomenclature of the vinegar and paste eels will have shown how complicated is the problem which it presents. Even modern nomenclators and systematists are divided amongst themselves, some supporting *Anguillula* Müller, 1786, with *rediviva* as type, others, *Anguillula* Hemprich and Ehrenberg, 1828, with *aceti* as type. If the International Rules of Zoological Nomenclature are to be

adhered to strictly, I do not think either position will be found to be tenable. Briefly summarized, the facts seem to be that *Anguillula* Müller, 1786, is due to a mistaken reading of the author's real intention, while *Anguillula*, 1828, is probably a nomen nudum—in any case, the slight available evidence suggests that the type (*fluviatilis*) is not congeneric with the vinegar and paste eels. To accept either of these names is to violate the principles of nomenclature, the strict application of which would demand a new genus altogether. An argument against making a new genus is that the name *Anguillula* has long been in use and is now universally recognized, and a new name would merely cause additional confusion. Against this can be set the following points:

(1) The universal agreement over the name conceals within itself a marked disagreement as to which *Anguillula* is the valid one, and along with this goes an equally marked disagreement as to what is the type. Since each of the conflicting parties can reveal genuine flaws in the reasoning of the other, there seems little hope of uniformity. Not even an *ex cathedra* decision from the International Commission can ensure universal acceptance (*v.* "IX^e Congrès international de Zoologie" [16], p. 881 (68): *Intemperate Language*). It is surely desirable to have a genus and a genotype which are acceptable to all.

(2) Genera are already on record with the names *Anguillina* and *Anguillulina*. While *Anguillina* Hammerschmidt, 1838, is regarded by Baylis and Daubney as *incertae sedis*, *Anguillulina* Gervais and van Beneden, 1859, seems fairly well established. Already, *Anguillula* and *Anguillulina* have given rise to family and subfamily names which are at first sight confusing (*e.g.*, *Anguillulina* from *Anguillula*).

(3) Finally, modern principles of nomenclature require a new name. This, of course, is the only valid reason for the change: the previous two points merely indicate advantages which would accompany it.

Taking these facts into consideration, it has been decided to create a new genus, *Turbatrix*, with *T. aceti* as type. As de Man has made *dryophila* a variety of *aceti*, and as this variety may come to be regarded as a separate species, I wish to restrict the type to the more common form found in vinegar, and to anticipate confusion I add to the name *T. aceti* the variety-name *aceti*. In order to secure an unpreoccupied name, the usual precaution has been taken of consulting Sherborn (Index

Animalium), Scudder (Nomenclator Zoologicus), the Index Zoologicus and subsequent parts of the Zoological Record.

GENERIC SUMMARY.

Turbatrix, 1927, genus novum, comprising¹ —

T. aceti (Müller, 1783) var. *aceti*, varietas nova, type by present designation. In vinegar.

T. aceti (Müller, 1783) var. *dryophila* (Leuckart, 1887) de Man, 1910.
In the slime-flux of the oak.

T. ludwigii (de Man, 1910). In the slime-flux of the oak.

T. rediviva (Linnaeus, 1767). In sour paste.

The generic diagnosis is that of de Man, 1910 (p. 362), based by him on the type species, *T. aceti*:

"In this genus the body is more or less slender and tapers considerably at both ends—especially posteriorly, where the tail terminates in a fine point. Cuticular striations extremely fine with narrow lateral alæ, bearing no bristles. Lateral lines present, arising in the region of the œsophageal bulb: one (and perhaps both) making several twists near its origin. Head rounded or truncated; lips present or absent, with one or two rings of papillæ. Buccal cavity small with a thin chitinous wall, which is hexagonal just behind the mouth but three-sided for the greater part, with outwardly bulging walls. The buccal cavity consists of two consecutive portions, the posterior of which bears a very small dorsal tooth and, in the type species, two subventral processes also." (The dorsal tooth is not a true generic character since it is absent in *T. rediviva*, *fide* Goodey, 1922.) "Æsophagus with posterior bulb, containing a valvular apparatus. Males non-bursate, with pre- and post-anal papillæ; two equal spicules with a single accessory piece. Vulva usually slightly post-median, the single ovarian tubule directed anteriorly; a posteriorly directed ovarium which opens as a blind sac into the vagina appears to

¹In 1913 de Man published a preliminary account of a new species of *Anguillula* ("ANGUILLULA SILUSIÆ n. sp., eine neue, in den sogenannten 'Bierfilzen' lebende, Art der Gattung ANGUILLULA Ehrh.," *Centralbl. f. Bakt. Parasit. u. Infekt.*, Abt. 2, Bd. 39, pp. 73 and 74). He describes this species as bearing resemblances to *A. ludwigii*, and promises an illustrated and more detailed account later, in the *Ann. de la Soc. roy. Zool. et Malacol. de Belgique*. So far, I have been unable to trace this fuller account, but it is highly probable that *T. silusiæ* should be added to the present list of species.

function as a receptaculum seminis. Ovoviviparous. Caudal glands absent."

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On *Arthrostoma felineum*, gen. et sp. nov., a Parasite of Cats.

By THOMAS W. M. CAMERON, M.A., D.Sc., Ph.D., M.R.C.V.S.

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THIS small species of Ankylostome worm was found in the small intestine of a golden cat (*Felis temminckii*) from Sumatra, in association with numerous specimens of *Ancylostoma caninum*, *A. braziliense* and *Strongyloides* sp. It has been experimentally transmitted to the domestic cat.

The *cuticle* shews not only transverse striations but numerous very fine longitudinal striations.

Like *Ancylostoma*, the body shews a distinct longitudinal torsion, and when the dorsal aspect of the cephalic opening is facing upwards, the posterior extremity is displaced laterally. The body is narrowed anteriorly, terminating in a pyriform buccal capsule which, as in *Ancylostoma*, opens dorsally. The anterior end does not form a hook-like bend as in *Necator* and forms allied to it.

The *buccal capsule* (figs. 1 to 5) at first sight shews distinct resemblances to that of *Arthrocephalus*, but this appearance is superficial. The capsule wall is composed of eight plates which do not completely articulate. The ventral part consists of a single large flat triangular plate (A), while the plate forming the base of the capsule (B) is in the shape of a truncated inverted cone. On the ventral aspect are two lancets of the usual *Ancylostome* type, while the thickened dorsal aspect is perforated (fig. 1) to carry the duct of the dorsal oesophageal gland. There is no dorsal cone, the duct opening in a manner identical with that in *Ancylostoma* and *Dochmoides*. The remaining six plates are paired. On the latero-ventral aspects of the capsule are two flat triangular plates (C, C') articulating with (A) on their ventral side. The base of the triangle articulates with a second pair of triangular plates (D, D') which articulate

with the basal cone (B). In the angle formed by (C and D) and (C' and D') lie the third, almost circular pair (E, E'), which join the basal cone (B) in such a manner as to form a V-shaped area free from cuticular material, at the base of which opens the duct of the dorsal oesophageal gland.

The mouth opening is a simple circular opening in the cuticle, unguarded by teeth, cutting plates or any other holding structures, as in the genus *Globocephalus* (fig. 4). This cuticle is supported by the apex of plate A and by plates C, C', E and E'.

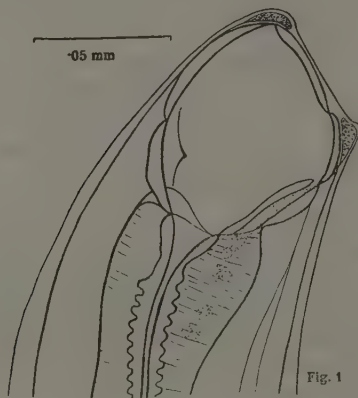


Fig 1.—*Arthrostoma felineum*: optical sagittal section of buccal capsule.

The oesophagus is similar to that of *Ancylostoma*. It is claviform and measures about 0.14 mm. in length with a maximum width of 0.035 mm. The nerve ring is situated just posterior to the middle. There are two cervical papillae in the usual place, and between and behind these the inconspicuous excretory pore is situated. Cervical and cephalic glands are as in *Ancylostoma*.

The male is about 3.25 mm. long with a maximum diameter just in front of the bursa of about 0.175 mm. The testicular tube originates just posterior to the middle of the body and runs anteriorly for a short distance. It is only very slightly convoluted, forming a double S before

it turns and runs almost directly to the ano-genital opening. The various parts are as in *Ancylostoma*.

The spicules are about 0.9 mm. long and are straight filiform rods, each within a transversely striated spicular sheath. These sheaths unite distally and the spicules form a single fine point (fig. 7). A small elongated accessory piece is present.

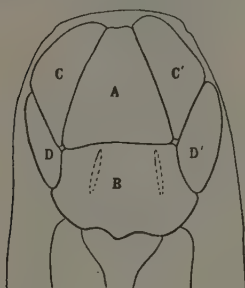


Fig. 2

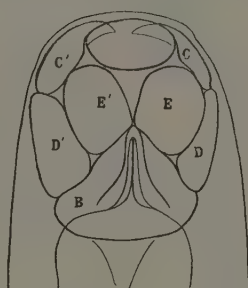


Fig. 3

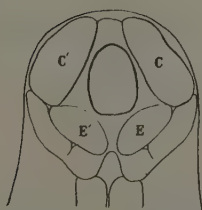


Fig. 4

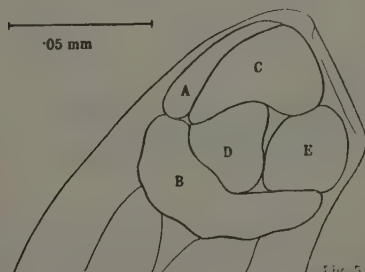


Fig. 5

Arthrostoma felineum: disposition of plates on buccal capsule. Fig. 2, ventral view. Fig. 3, dorsal view. Fig. 4, terminal view. Fig. 5, lateral view.

The genital cone (fig. 7) is large and possesses a ventral projection with incurved edges. The spicules lie in the groove thus formed.

The pre-bursal papillæ are conspicuous. The bursa (figs. 6 and 7) is of the usual *Ancylostoma* shape from which it differs only in details.

A very small dorsal lobe is present. The ventral rays are fine, narrow structures which do not diverge. The lateral rays are massive and pointed and all diverge widely. The externo-lateral is directed ventrally; the medio-lateral and the postero-lateral are directed dorsally. The externo-dorsal ray is thick at its origin from the main dorsal stem but rapidly narrows and the distal two-thirds is uniformly narrow. The dorsal ray is stout and bifurcates only near its tip. Each bifurcation divides and the medial portion redivides forming three digitations on each.

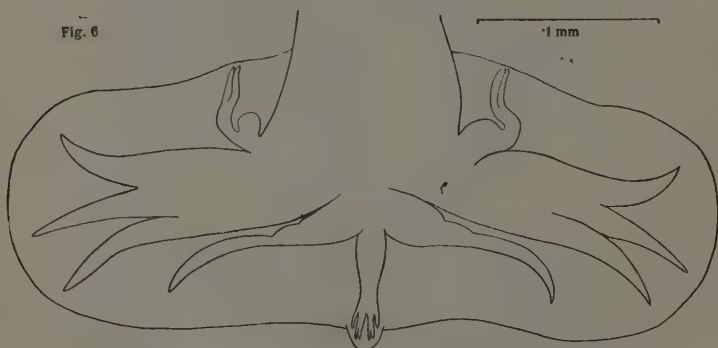


Fig. 6.—*Arthrostoma felineum* : bursa of male spread out.

The female is about 4.5 mm. long with a maximum diameter of about 0.2 mm. The tail (fig. 8) is abrupt and the body substance is carried through the posterior portion to form an elongated sharp spike. Just anterior to this is a pair of small caudal papillæ. The anus is similar to that in *Ancylostoma* and is situated about 0.1 mm. from the base of the spike.

The vulva (fig. 9) is a transversely situated slit, dividing the body in the ratio of 11 : 5, *i.e.*, it is situated just posterior to the junction of the middle and posterior third. It is protected by a small flap of cuticle,

which, however, does not project. This flap is reinforced by a wedge of denser cuticular material. The vulva communicates with a backwardly directed vagina which after an S-shaped course joins a paired ovejector. This is similar to that seen in *Ancylostoma*, but is somewhat longer.



Fig. 7

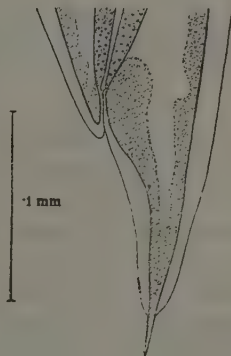


Fig. 8



Fig. 10

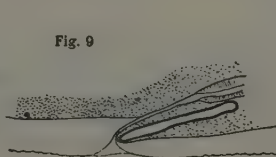


Fig. 9

Arthrostoma felineum: Fig. 7, posterior end of male shewing spicules, genital cone and cloaca. Fig. 8, posterior end of female, shewing anus and terminal "spike." Fig. 9, vulva. Fig. 10, vulvar papilla.

The ovejector is situated somewhat on the left side of the body, and at right angles and lateral to it is seen a single papilla (fig. 10) which enters the cuticle, but only causes a very slight swelling to result. There is no corresponding papilla on the other side and it has been seen in all the specimens examined.

The ovejector is of the typical *Ancylostoma* form, consisting of a relatively very long *pars haustrix* and a short *pars ejectrix*. Both uteri, on

the other hand, are relatively short and each is modified to form a small seminal receptacle at the point where it joins the ovarian tubule by a very short oviduct. The genital coils lie in a longitudinal direction except in the middle of the body (anterior to the ovejector) where they are mainly transverse.

The eggs, which are deposited in the four-cell stage, are of the usual Ankylostome type and measure about 55μ by 25μ .

DISCUSSION.

This species is peculiar in several respects. As in *Arthrocephalus*, the buccal capsule consists of imperfectly articulated plates; but, whereas in that genus there were six such plates, in this there are eight. Moreover there is no dorsal cone present, while the usual pair of ventral lancets is seen. In *Arthrocephalus* a conspicuous dorsal cone is present and there are no ventral lancets. The details of the bursa also differ. In *Arthrocephalus* the medio-lateral ray is directed anteriorly; while in this species it is directed dorsally. The shape of the externo-dorsal ray differs considerably in the two species. The most unusual feature, however, is the presence of an asymmetrical papilla at the level of the vulva.

The absence of any form of armature protecting the actual mouth opening, together with the general shape of the buccal capsule, suggests affinities to *Globocephalus*. In that genus, however, the buccal capsule consists of a single structure and the complicated system of articulated plates is absent.

The differences between this new species and these two genera seem to be as pronounced as those existing between the other genera of the Ancylostomidæ, and accordingly it is given the name *Arthrostoma felineum*. It may tentatively be differentiated from other genera of this family by the articulated buccal capsule (composed of eight plates) with no dorsal cone and with no armature to the oral aperture.

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On the Parasitic Development of *Monodontus trigonocephalus*, the Sheep Hookworm.

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Nomenclature.

A CERTAIN amount of confusion still exists as to the terminology to be adopted in discussing the various stages in the life cycle of the Nematoda. This appears to be largely due to a difference of opinion as to the termination of each stage.

After a larva has reached a certain size, it commences to change in form and completes this process by shedding its cuticle. This change in form is the *lethargus*. It may or may not immediately escape from the cast cuticle, but when it does, the ecdysis is complete. The form which emerges is morphologically identical with the form inside the cuticle *after* the completion of the lethargus.

This accordingly gives a double choice as to the exact end of the stage. It may be *during* the lethargus, when the morphology of the form is changing, or it may be at the moment when the larva leaves the cast cuticle. The interval between these periods is slight in some cases but is considerable in the case of the infective stage. As the physiological end of the stage seems to coincide with the lethargus, I have accordingly based my nomenclature on it.

The "ideal" life cycle of a nematode (of the hookworm group at least) appears to be as follows:—

The *first stage* larva emerges from the egg and is provided with an œsophagus of the so-called rhabditiform type, *e.g.*, an œsophagus with a more or less cylindrical anterior portion connected by means of a narrow commissure with a spheroid posterior portion. The oral aperture is connected to the anterior end by means of a cylindrical buccal tube in the case of the hookworms.

After a lethargus and moult, the *second stage* appears, similar in general morphology to the first but larger in size and possessing a *double* instead of a single lateral line. This stage is also free-feeding. After a *second* lethargus, the *third* or *infective* larva is seen, as a rule still within the cuticle of the old second stage. This form is not free-feeding and the buccal tube is absent, although a modified constriction is still present between the anterior and posterior parts of the œsophagus. This stage normally does not cast the old cuticle until on the point of entering the body (either by the mouth or by the skin). Inside the body it continues to grow.

After a *third* lethargus and moult, the *fourth* stage larva appears, characterized by the presence of a temporary buccal capsule, which in the known hookworms is more or less spherical and provided with internal lancets. This form grows and after a *fourth* lethargus gives rise to the *fifth* or *adult* stage. This stage grows to its maximum size without further alteration in shape and without any other moults.

There are accordingly (excluding the egg) *five* stages, separated by four lethargic periods, each of which, sooner or later, culminates in a moult. Of these stages, two are free-living, one is transitional and two are parasitic.

This typical life history is followed in detail by the hookworm genera *Ancylostoma*, *Monodontus* and *Necator*, as well as by a number of species of Trichostrongylidæ (where of course both temporary and permanent buccal capsules are absent). Close approximations to it are seen in other species of Strongyles, including probably the Protostrongylidæ. There are of course exceptions to the rule. In *Ollulanus* for example, although all five stages are represented in the life cycle, one or possibly two moults take place *in utero*. In *Syngamus*, Ortlepp finds that the first stage is entirely suppressed and the third stage emerges from the egg.

Nevertheless there is such a close general agreement within the group of the bursate nematodes, that it is considered legitimate to take this cycle as typical and to use it as the standard for purposes of comparison.

This may be shewn thus:—

Egg

1st stage larva (1st non-parasitic stage).

1st lethargus.

1st ecdysis.

2nd stage larva (2nd non-parasitic stage).

2nd lethargus.

3rd stage larva (infective stage).

2nd ecdysis.

3rd stage larva (1st parasitic stage).

3rd lethargus.

3rd ecdysis.

4th stage larva (2nd parasitic stage).

4th lethargus.

4th ecdysis.

Adult.

The Third Stage Larva.

The life history of *Monodontus trigonocephalus* follows almost identical lines to that of *A. duodenale*. The morphology of the first three stages has previously been described by Hesse (1923) and the biology of the infective larva has been studied by the present writer (1923). The work in this preliminary article has been continued and it is necessary to modify one statement made therein. In all the writer's earlier experiments on cultivation, the cultures had been made by the Leiper Petri dish method, the actual mixture of eggs and fæces in the lower part of the Petri dish being of the consistency of thick cream. It had been found that larvæ of human hookworms would leave such a mixture and migrate to the blotting paper on the lid of the Petri dish. *Monodontus* larvæ invariably failed to climb from this mixture. It was later found, however, that if sufficient fæces and charcoal were added to make an almost solid mass, infective larvæ of *Monodontus* would leave the fæcal culture after a few days and climb on to the lid. As sheep fæces normally are of a much more solid nature than those of man or the dog,

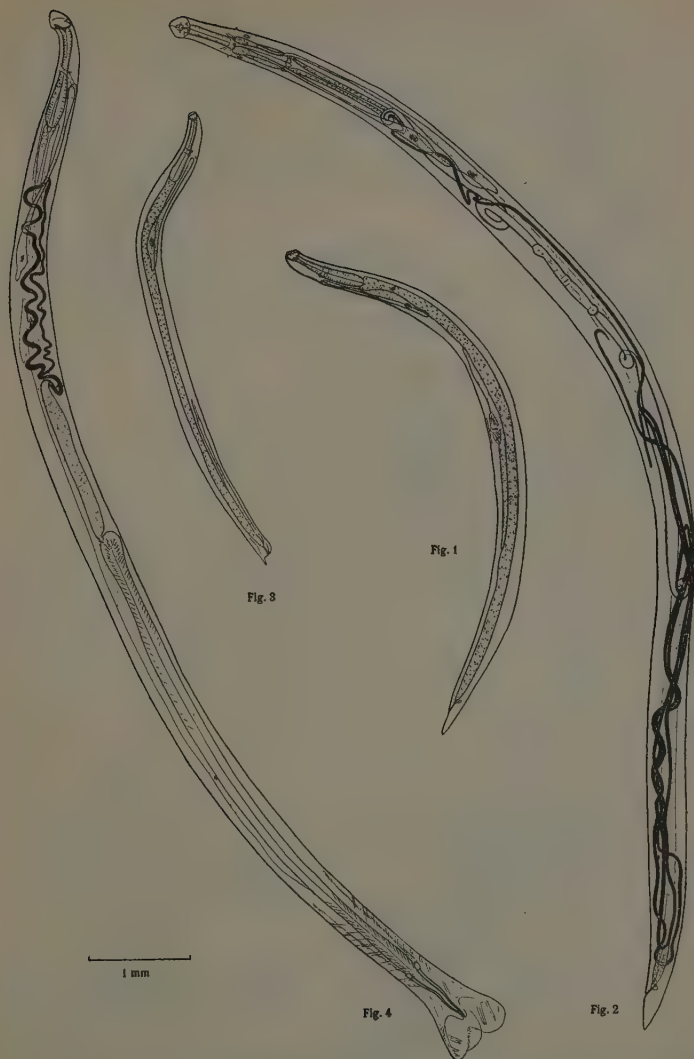
it would seem that this is an adaptation of their biology specially designed to suit their normal environment. The earlier culture media were, of course, abnormally fluid in consistency.

It was found, however, that the usual technique of allowing the surface of the culture to dry and then flooding it gently with warm water, remained the best method of isolating the infective larvæ in numbers sufficiently large for study.

Experiments on skin penetration, using the Goodey floating raft technique, were continued, but in no case did the larvæ ever penetrate the skin. In addition to skin from newly born rats and mice, skin from between the claws and from the mouth of sheep as well as various kinds of mucous membrane were tested. The only occasion on which more than the usual activity was shewn was when a piece of small intestine from a freshly killed sheep was used. On this occasion, the larvæ burrowed down among the glands; no penetration took place however.

The recent work of Yokogawa (on *Ancylostoma*) and Fülleborn (on *Dochmoides*) suggests that in these forms (both of which actively penetrate skin) the passage through the blood stream, which has hitherto been accepted as an essential part of the life cycle, should be interpreted as a convenient means of reaching the intestine—possibly also as a “philogenetic reminiscence,” as Fülleborn suggests, of a time when an intermediate host played an essential part in the life cycle. If the larvæ are swallowed, they need never leave the alimentary canal but can continue their development, at first in the intestinal glands, subsequently in the lumen of the canal itself. The lung-passage is only necessary in the case of those larvæ which have entered by the skin—although Fülleborn shews that a considerable amount of development may actually take place in the lungs, he regards this as evidence of “survival habits” rather than an essential part of the development.

In the case of the sheep hookworm, opportunities for infection through the skin must necessarily be limited; and although this may be the main method of infection in animals with unprotected limbs, it would seem, even if the larvæ could penetrate the skin, to be at best a subsidiary method in the ungulates where hooved feet and oily



Monodontus trigonocephalus.

Fig. 1.—Old female fourth stage larva. Fig. 2.—Young adult female. Fig. 3.—Old male fourth stage larva. Fig. 4.—Young adult male. (All to same scale.)

wool or hair would oppose penetration. Moreover, the hosts of the skin penetrating forms are not grass eaters, whereas the food habits of sheep are such as to offer the larvæ a much easier and a much more certain method of entering the body.

The evidence, both theoretical and experimental, is accordingly in favour of this species being unable to penetrate skin.

The Fourth Stage Larva.

I have been unable to obtain specimens shewing the parasitic development of *Monodontus* prior to the young fourth stage larva, i.e., forms shewing the development of the provisional buccal capsule.

The youngest stage seen was already 2.3 mm. long and 0.13 mm. broad.

The cuticle is transversely striated. Cervical papillæ are present at about the level of the middle of the œsophagus, but there are no papillæ present in the region of the tail.

The mouth capsule (fig. 5) is almost spherical in form with the aperture directed in a termino-dorsal direction. In the immature fourth stage the diameter is about 0.06 mm., but as the larva grows this increases to 0.1 mm. The wall reaches its maximum thickness at the ventral portion of the base. Three teeth are present—a large dorsal tooth with a somewhat concave dorsal aspect and a convex ventral aspect, and a pair of triangular-shaped ventral teeth. There is no dorsal cone as in the adult forms.

On the cuticle on the outside of this buccal capsule are three pairs of papillæ carrying nerve endings—one pair lateral, the others dorso-lateral and ventro-lateral in position. The actual opening of the mouth capsule is unguarded by any form of cutting plates or teeth (fig. 6) and is circular in outline.

This buccal capsule corresponds very closely to the similar stage observed by Looss in the case of *A. duodenale* and by Stiles and Goldberger in the case of *Necator americanus*. Looss, however, described *two pairs* of teeth as being present in the mouth capsule, whereas in *Monodontus* the dorsal tooth is single. In the case of *A. ceylanicum* as previously depicted by Vevers (1922) (fig. 9, which is drawn from

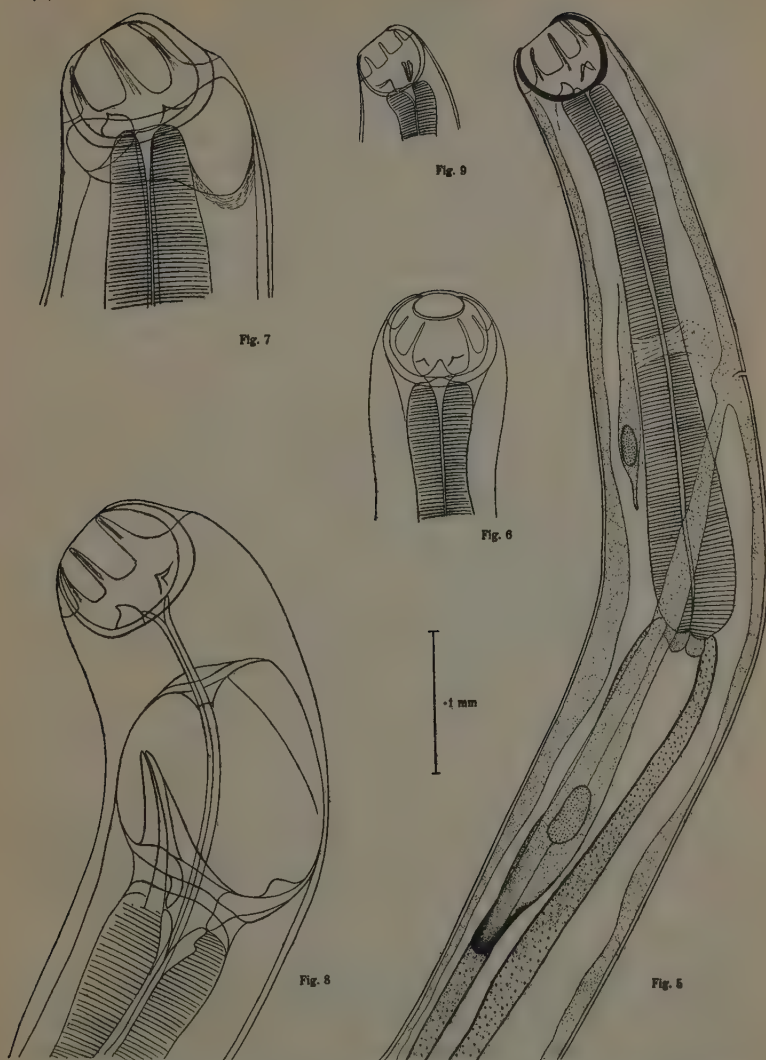


Fig. 5.—Cephalic region of young fourth stage larva (lateral view). Fig. 6.—Dorsal view of buccal capsule of same larva. Fig. 7.—Commencement of permanent buccal capsule. Fig. 8.—Completion of permanent buccal capsule. Fig. 9.—Lateral view of buccal capsule of fourth stage larva of *A. braziliense* (*A. ceylanicum*).

one of his specimens), the arrangement is similar to that in *Monodontus*, but the shape of the teeth is different. The dorsal tooth is a large pyramidal tooth with the apex directed *ventrally* and the ventral teeth are elongated and rod-like. The mouth capsule is also considerably smaller than in *Monodontus*. In the preliminary note published by Stiles and Goldberger, the provisional buccal capsule of *Necator* closely resembles that of *A. ceylanicum*.

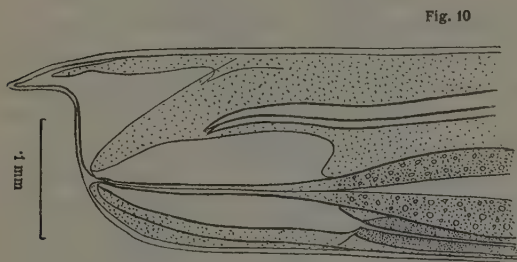
The œsophagus is 0·4 mm. long with a maximum diameter of 0·06 mm. It is similar in shape and construction to that seen in the adult. The dorsal œsophageal gland opens into the buccal capsule at the *base* of the dorsal tooth while the two latero-ventral glands open into the lumen of the œsophagus at about the level of the nerve ring.

The nerve ring occurs at about the level of the middle of the œsophagus while the excretory pore is just posterior to this. Connected to the excretory pore are two cervical glands similar in appearance to those seen in the adult but relatively shorter in length. Cephalic glands are also present but these, although longer than the cervical glands in the adult, are considerably shorter in the larva. Their nucleus, however, as in the adult, lies just posterior to the middle of the œsophagus. It was not possible to observe their pores. The intestine and œsophago-intestinal valves are similar to those seen in the adult. The rectum is a short straight tube, opening in the form of a transverse anus, about 0·01 mm. from the posterior end of the body. The tail of the young form is bluntly pointed. It changes considerably in outline as the larva grows and the sexual characters commence to develop. In the young fourth stage the genital rudiment is still found as an undifferentiated group of cells, the position of which, however, differs in various specimens. It is placed centrally in the future females, towards the posterior region of the body in the males.

The Development of the Adult Buccal Capsule.

The adult buccal capsule appears as two small vacuoles just posterior to the provisional buccal capsule. The smaller of these vacuoles is on the dorsal aspect, the larger on the ventral aspect, of the anterior extremity of the œsophagus. These continue to grow (fig. 7) and finally unite laterally to form a continuous cavity round the œsophagus.

Subsequent growth is in an antero-posterior direction and ultimately the provisional capsule is entirely detached from the œsophagus. The anterior portion of the œsophageal lining being composed of cuticular material remains, but the surrounding muscular and glandular substance disappears. Meanwhile, the cavity has had a layer of cuticular material deposited on its inner surface (fig. 8) and this homogeneous sheet is the future adult capsule. It is thickened posteriorly but at the time of ecdysis is still very thin anteriorly. There is no trace of the deposition of separate cuticular plates which unite secondarily, the whole capsule being homogeneous.



Monodontus trigonocephalus.

Fig. 10.—Tail of male fourth stage larva.

The dorsal cone is formed by an ingrowth of cuticle to surround the anterior part of the dorsal gland of the œsophagus, which continues to form the core of the cone. The buccal teeth arise from thickenings in the cuticle of the ventral wall of the capsule.

The whole capsule is covered with true cuticle from which the actual mouth opening is formed and in which the cephalic papillæ lie.

The provisional buccal capsule becomes completely detached and is then cast off, together with the anterior portion of the œsophageal lining (fig. 8).

The Development of the Male Organs.

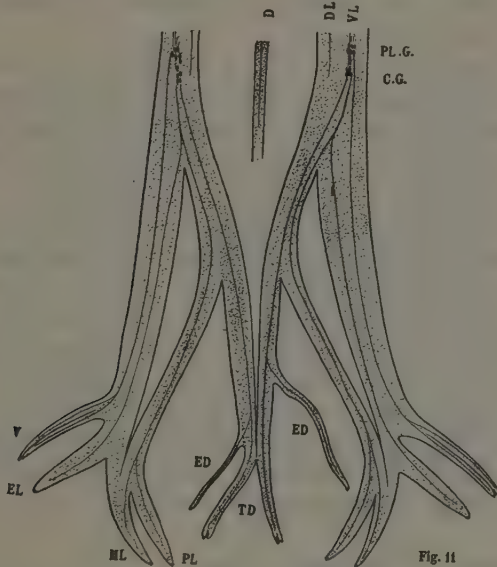
The genital rudiment of the male proliferates more actively in an

anterior than in a posterior direction, but it is not possible to say exactly which portions are responsible for the various parts of the adult male system. In the very young adult, the testicular tube commences at the level of the top of the seminal vesicle and passes anteriorly in an undulating fashion, reverses a short distance posterior to the end of the œsophagus and, still forming transverse coils, proceeds to join the seminal vesicle in a sigmoid bend. The anterior loop regarded by Looss as characteristic of *A. duodenale* is not present. The seminal vesicle is not spindle-shaped as in *Ancylostoma* but has almost parallel sides. It narrows abruptly to form the ejaculatory duct at the level of the top of the cement glands which are about half the length of the body. Of the external sexual organs, the genital cone is the first to develop and in the late fourth stage larva is seen to extend almost to the posterior end of the body (fig. 10). Later the bursa grows more rapidly and extends some distance beyond the genital cone. This growth of the genital cone and bursa gives the late fourth stage male larva its characteristic shape. The rectum is seen extending as a long tube in the centre of the cone joining the fourth stage anus to the adult anus at the base of the cone. This tube is detached with the cast cuticle. The spicules develop from a group of cells dorsal to the end of the intestine. Their retractor muscles are very long and originate in the cuticular muscles. The development of rays is difficult to follow in the fourth stage larva owing to the very crumpled bursa which cannot be straightened out on account of the inflexible larval cuticle. In the young adult, however, it is seen that all the rays are prolongations of the lateral bands. At this stage it is also possible to follow the development of their nervous system.

The lateral bands (fig. 11) split some distance before the origin of the rays into two branches—a ventral and a dorsal. The ventral branch, which is the larger, forms the ventral rays, the externo-lateral and part of the medio-lateral.

The dorsal branch splits again and forms, from its ventral part, the postero-lateral and part of the medio-lateral rays; while the dorsal branches from each side of the body give off the externo-dorsal rays and then fuse to form the stem of the termino-dorsal ray. Their tips remain separate, however, to form the branches of this ray.

The ganglia in the posterior end of the body are similar to those found in *Ancylostoma*. The ventro-lateral nerves give rise to three more or less distinct groups of nerve cells—the lumbar, the post-lumbar and the costal ganglia—but in *Monodontus* the two last lie very close together.



Monodontus trigonocephalus.

Fig. 11.—Diagram shewing evolution and innervation of bursal rays in newly moulted adult. (D=Dorsal Nerve; DL=Dorso-lateral nerve; VL=Ventro-lateral Nerve; PL.G. = Post-lumbar ganglion; C.G. = Costal ganglion.)

As in *Ancylostoma*, however, the nerves for all the rays arise from the post-lumbar and costal ganglia. The former gives rise to the common nerve to the ventral rays (which arises from the ganglion in common with the commissure joining it to the anal ganglia). This nerve gives rise to bifurcations which supply the ventro-ventral and latero-ventral rays. The remaining nerves rise from the costal ganglion. One trunk running down the ventral part of the lateral band supplies

the externo-lateral ray. Close to its origin it gives rise to another nerve running down the dorsal branch to supply the remaining lateral rays. Running parallel to this nerve, but apparently originating independently from the ganglion, is the nerve to the dorsal and externo-dorsal rays. This nerve does not unite with the corresponding nerve from the other side. I was unable to observe the terminal course of the dorso-lateral nerve, which in *Ancylostoma* also appears to enter the termino-dorsal ray.

The prebursal papillæ in the male do not arise from the lateral bands but from prolongations of the ventral band and the pulvillus post-analis. The caudal papillæ in the female, on the other hand, arise from the lateral bands. Neither pair of papillæ project above the surface of the cuticle.

These two sets of papillæ do not appear to be homologous as the nerve supplying the male papillæ rises from the same commissure as does the nerve to the ventral rays; whereas the nerves to the female papillæ are the terminal portions of the main ventro-lateral trunk. Accordingly the caudal papillæ in the female are equivalent either to the entire system of male rays or to the termino-dorsal rays only. If the dorso-lateral nerve, in addition to the terminal branch of the ventro-lateral nerve, supplies the dorsal rays, the latter would appear to be the case; the other ray-nerves would be merely outbranches of the ventro-lateral, not represented in the female.

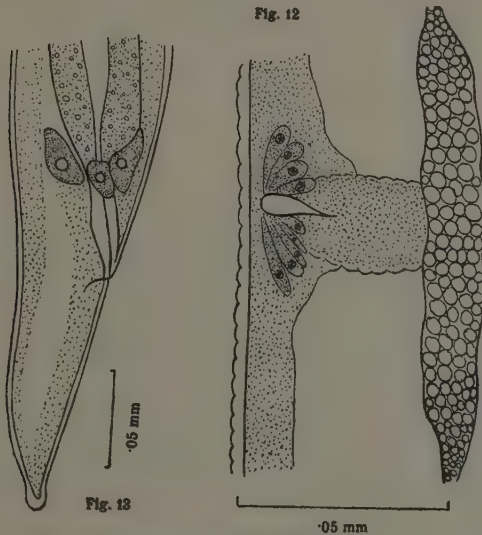
The Development of the Female Organs.

The genital rudiment, which at the beginning of the stage is an undifferentiated mass of cells, proliferates actively at both ends and the two columns of cells thus formed grow into the two uteri and ovaries. The central portion forms the ovejectors. The vagina and vulva (fig. 12) are formed from cells in the wall and they unite secondarily with the ovejectors.

The course of the ovarian tubules can be clearly seen in the newly moulted adult (fig. 2). The *anterior* uterus passes forward for a considerable distance, looping once on itself as it does so, to the anterior quarter of the body where it joins the ovarian tubule which runs almost to the posterior region of the body in an undulating

fashion. There it turns and proceeds anteriorly, almost parallelly to itself, until it reaches the centre of the posterior uterus, where it again turns and almost immediately terminates in a rounded point.

The posterior uterus, also looping on itself, proceeds posteriorly where it joins the ovarian tubule by a short oviduct. The ovarian tubule proceeds anteriorly for a short distance but quickly turns and proceeds



Monodontus trigonocephalus.

Fig. 12.—Formation of vulva. Fig. 13.—Tail of female fourth stage larva.

in an undulating fashion to the posterior end of the body—but on the opposite side of the intestine to the other ovary. There it turns and proceeds parallelly to itself to the level of the first turn. It runs forward to about the middle of the inferior uterus where it terminates in a blunt point.

As the adult continues to grow, the uterine loops increase in length and the ovarian coils in complexity.

Biology.

The biology of the fourth stage larva is still unknown. All the forms discussed in this paper were recovered from the small intestine, and from the mouth of one was removed a detached villus. Apparently this stage feeds on the mucosa of the intestinal wall—as has been found by Looss to be the case with *A. duodenale*. The fact that the digestive and excretory systems are of the adult type suggests that its habits in the host would be similar. The relatively small size of the buccal capsule would, however, make it much less dangerous than the adult form.

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On *Tylenchus graminis* (Hardy 1850) Marcinowski 1909.

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INTRODUCTION.

HARDY (1850) gave a description of some eelworms occurring in leaf-galls on the grass *Festuca ovina* and named them *Vibrio graminis*.

Marcinowski (1909), p. 126, dealt very briefly with Hardy's account and brought the worms into the genus *Tylenchus*, at the same time admitting the arbitrariness of such a procedure. She says that she had no means of making a morphological comparison of the worms with *Tylenchus tritici* owing to lack of material. Micoletzky (1921), p. 546, listed it as a species of indeterminate value and specificity.

The writer has been fortunate in obtaining a number of galls from the leaf-blades of *Festuca duriuscula*, a species very closely related to *F. ovina*. With this material experiments have been carried out in pots sown with seed of *F. duriuscula* and *F. ovina* and infected with dried galls resulting in the production of new galls. From these the adult worms have been obtained and studied in comparison with the adults of *T. tritici*. The second stage larvæ of the two species have also been compared to determine whether any specific differences could be established. The investigation shows that *Tylenchus graminis* is a true and distinct species.

The writer is greatly indebted to Mr. G. Wallace and his son, Dr. G. Wallace, of Edinburgh, who very kindly collected and sent him the gall-bearing grass on two occasions. Thanks are also due to James MacDonald, Grass Specialist, Harpenden, for his kindness in supplying the grass seed used in the experiments.

EXPERIMENTAL.

Early in May five 6-inch pots were almost filled with pasture soil which had been partially sterilised by heat and after sieving mixed with about 10 per cent. of silver sand. Seed of *F. duriuscula* was sown in three pots and of *F. ovina* in two pots. One pot of each species was left uninfected as control and the others were sown with dried galls distributed evenly amongst the seed. Seed and galls were lightly covered with sifted soil and sand and after watering the pots were placed in a warm greenhouse. Germination took place in a few days and when the seedlings were well established the pots were put in the open air on a plot covered with ashes.

Galls were found on several grass blades on the infected pots early in August and by the middle of September had become very numerous on one of the pots of *F. duriuscula*.

Both species of *Festuca* used are fine grasses with bristle-like leaf-blades which are permanently folded and at their widest are scarcely a millimetre broad. The galls vary in size and number and there may be one or more on a single blade. The small ones sometimes measure less than 1 mm. in length by about 0.5 mm. in width, whilst larger ones may measure up to 3 mm. or 4 mm. in length by 1 mm. to 2 mm. in width. As the galls are of a darkish purple colour and occasionally have a rather irregular surface they form conspicuous bodies especially when more than one is present on a blade. In this case the latter often looks as though it possessed dark swollen joints.

When a portion of leaf-blade carrying a gall is placed in a drop of water and the edges of the blade are forced apart by needles the gall is generally to be seen lying to one side of the midrib; occasionally in the case of large galls they may be found on both sides of it. On touching the surface with needles it is found to be hard and on breaking into it a bright purple colour floods out into the water. Examination under the microscope shows that the cells composing the wall of the gall are filled with this purple liquid. It is most probably an anthocyanin compound in solution, for when galls are broken down in a weak acid, the purple is changed to a bright red colour, whilst in a weak alkaline medium the colour is first purple but soon changes to a greenish blue.

The worm or worms lie within the hollow cavity of the gall and may be floated out when a gall is broken down in water. It is then a simple matter to pick them up and mount them for microscopic examination. Several small galls have been found which only contain a single adult male or female worm. In larger galls two or three adult worms of each sex have been found together with eggs and larvæ.

For the comparison of the worms with *Tylenchus tritici* examples of the latter have been obtained from greenish unripe galls in an infected ear of rye and by soaking out dried unripe galls from wheat.

MORPHOLOGY.

The adults of *Tylenchus graminis* are very similar in general appearance and structure to those of *T. tritici* but are of smaller dimensions than the latter. In both sexes the body tapers anteriorly and posteriorly as in other members of the genus. The cuticle is transversely striated and at the head end there is a flattened boss of cuticle, the edges of which gently slope and join it to the body. The alimentary canal has the same structure in both sexes and begins with a small stylet about 0.01 mm. long, followed by the œsophagus, which is readily divisible into three principal parts; an anterior portion rather less than half the length of the whole œsophagus, a central oval or rounded muscular bulb, and a third part which is first narrow and then expands into a broad spatulate organ. The first part is glandular on its dorsal side and a short duct connects it with the base of the stylet. The third part also is glandular and in its fine granular substance two large nuclei may often be seen. A narrow cuticular lumen traverses the whole œsophagus and leads into the intestine which runs almost to the end of the body and is connected by a short rectum with the anus. The excretory pore is situated a little behind the level of the median muscular œsophageal bulb.

Female Characters. Principal measurements: total length, 1.87 mm. to 2.7 mm.; greatest breadth, 0.1 mm. to 0.13 mm.; anterior end to vulva, 1.63 mm. to 2.32 mm.; anus to tip of tail, 0.07 mm. to 0.08 mm.; stylet, 0.01 mm.; œsophagus, 0.22 mm. to 0.25 mm.; anterior extent of gonad from vulva, 1.25 mm. to 1.8 mm.; eggs, 0.071 mm. to 0.083 mm. long by 0.033 mm. to 0.037 mm. wide with rounded ends.

Mature females of *T. tritici* are much larger than the above dimensions indicate for *T. graminis*. Marcinowski (1909) gives their length as 4.10 mm. to 5.23 mm., Byars (1920) gives it as 3.42 mm., whilst the writer obtained a female from a green gall on rye having a length of 4.46 mm.

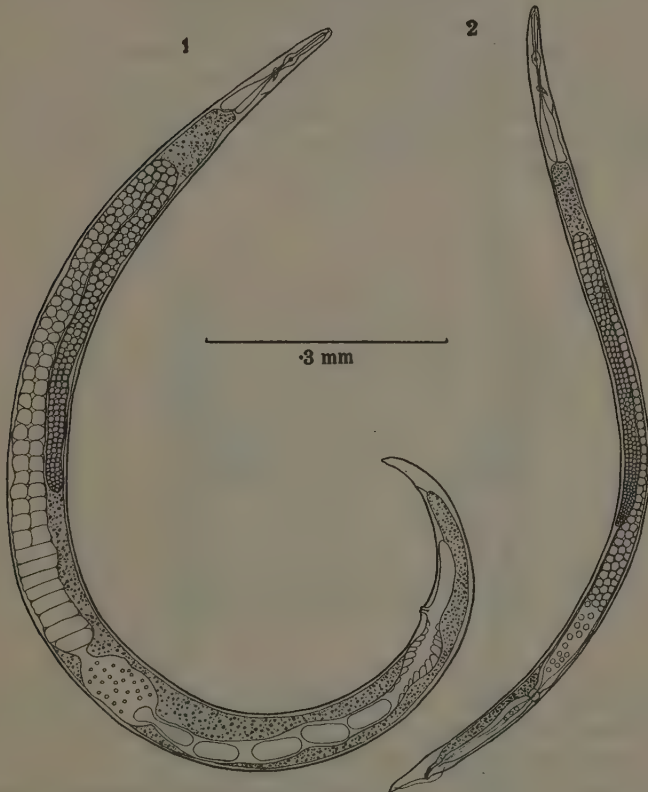
The vulva has rather prominent lips and is placed far back on the ventral surface of the body. It leads directly into the uterus which is first narrow, then dilates somewhat and then becomes tubular. Its wall is made up of large polygonal cells. Proceeding anteriorly there is a constriction of the tube leading into a fairly broad expansion, the receptaculum seminis, which is separated from the ovary proper by a further constriction of the wall. The ovary is continued forward in the body almost to the beginning of the intestine, where it folds back upon itself for a considerable distance and gradually becomes narrower. There is a post-vulvar blind sac or posterior extension of the uterus which frequently contains spermatozoa. The eggs are laid in a well-segmented condition.

Male Characters. Principal measurements: total length, 1.12 mm. to 1.58 mm.; greatest width, 0.05 mm. to 0.075 mm.; anus to tip of tail, 0.07 mm. to 0.09 mm.; stylet and œsophagus as in female; anterior extent of gonad, 1.02 mm. to 1.22 mm.; length of spicule, 0.045 mm.; length of gubernaculum, 0.013 mm.

Males of *T. tritici* are considerably larger than these measurements indicate for *T. graminis*. Marcinowski (1909) gives the length as 1.91 mm. to 2.5 mm., Byars (1920) gives it as 2 mm. to 2.5 mm. The writer's own measurements agree well with these, the males found by him measured 2 mm. to 2.35 mm.

The gonad is single and is anteriorly reflexed backwards to about half its length. The vesicula seminalis is clearly defined and has stout walls. There are distinct caudal alæ which arise a short distance anterior to the anus and extend on either side in a ventro-lateral position to their insertion a little in front of the tip of the tail. The latter is variously shaped; sometimes it is like an irregular blunt peg and sometimes it is slightly bifid. There is a certain amount of variation also in the distance from the tip of the tail at which the caudal alæ are inserted; they may reach practically to the tip or be inserted some little distance anterior to it.

In most morphological studies on nematodes close attention is paid to the shape, size and structure of the spicules and associated organs as they are generally recognised as giving characters of value for the



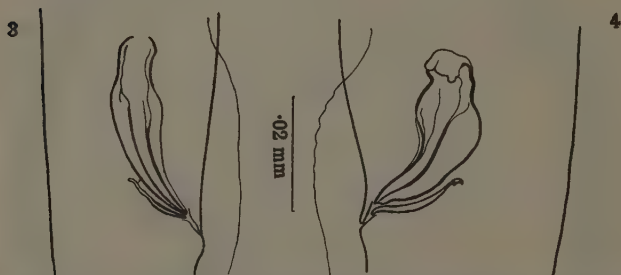
Tylenchus graminis.

Figs. 1 and 2.—Mature female and male showing chief anatomical features.

determination of specific similarities and differences. The writer has carefully examined the spicules and gubernaculum under oil-immersion lenses in both *T. graminis* and *T. tritici*, and drawings of a single spicule

and the gubernaculum in each species made to the same magnification are shown in figures 3 and 4.

The spicules in each species are gently bowed with the concave surface on the ventral side and the tips are pointed. In each there are two distinct ridges along the ventral surface extending from the tip to the level of the broadest region. In *T. graminis* the spicule is of a more slender build than in *T. tritici*, which at its broadest part is much wider than the corresponding region in *T. graminis*. Another important difference is that in *T. graminis*, when seen in lateral view, the anterior end of the spicule appears to be open with the dorsal and



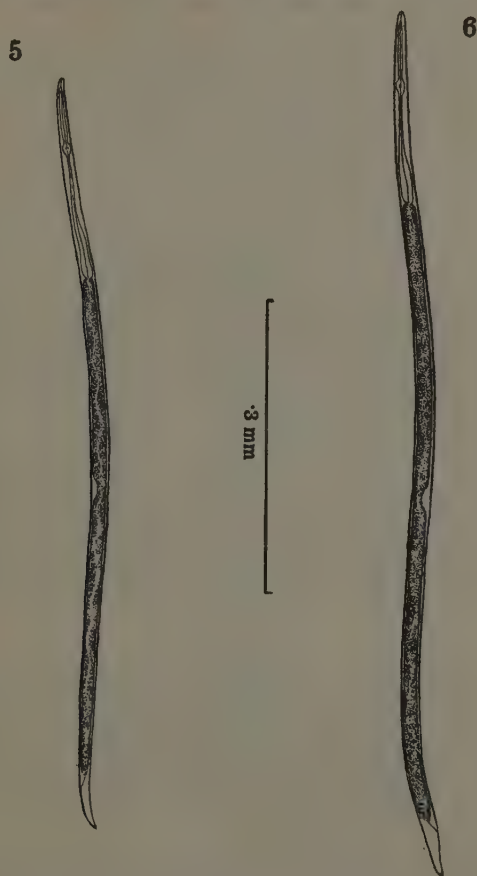
Figs. 3 and 4.—Lateral view of a spicule and the gubernaculum in *Tylenchus graminis* and *Tylenchus tritici* respectively.

ventral edges curving inwards towards each other slightly, whereas in *T. tritici* the dorsal side of the anterior end is flexed ventrally, giving the appearance of a kind of flap.

The gubernaculum in each species, when viewed laterally, appears simple, but in a ventro-lateral view it is seen to have a rather triangular shape with the broader part underlying the points of the spicules and the apex directed dorsally.

Larvæ.—As in *T. tritici* the eggs laid within the galls hatch and give rise to small first stage larvæ which soon grow and become second stage larvæ with probably an intervening moult. It is by means of these

second stage larvæ which are capable of long periods of quiescence in a dried state that the life cycle of the worms is carried on as they revive and become active when the galls are soaked in water. They



Figs. 5 and 6.—2nd stage larvæ of *Tylenchus graminis* and *Tylenchus tritici* respectively.

are very closely similar in appearance, structure and proportions to the same stage larvæ of *T. tritici*, but are slightly smaller.

The difference in size between the larvæ of the two species is the only one that could be discovered after very careful examination under high power magnification. Anatomically they are practically identical; even the tips of the tails have the same shaped pointed process.

Measurements have been made of a number of larvæ obtained from soaked galls and from fresh galls taken straight from the plants. The larvæ have first been killed by gentle heat in a drop of water and then covered with a coverslip. Thirty such larvæ selected at random gave an average length of 0.728 mm., with a range of 0.67 mm. to 0.79 mm., and a breadth of 0.014 mm. to 0.018 mm. at the widest point. These figures are rather smaller than those for the second stage larvæ of *T. tritici*, which from the writer's measurements have an average length of 0.88 mm. and a range of 0.8 mm. to 0.95 mm. and a breadth of 0.15 mm. to 0.2 mm. Marcinowski gives the length as about 1 mm., whilst Byars gives the average length as 0.869 mm. and a range of 0.77 mm. to 0.966 mm., with slightly smaller figures for specimens obtained from Chinese galls in which the average length of 0.793 mm. was found and a range of 0.658 mm. to 0.910 mm.

These figures indicate that although the larvæ of *T. graminis* come within the lower limits of the measurements for *T. tritici* they do not reach the upper limits of length and that the average is smaller. This may be taken, in conjunction with the differences shown by the adults, as indicative of a real specific difference between the two species.

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A Study of the Helminths of Dogs and Cats of Aberystwyth, Wales.

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WHILE carrying out an intensive survey of the helminths parasitic in domestic animals at Aberystwyth, an opportunity was afforded the writer to examine the dogs and cats taken to the local police station for destruction by the lethal chamber process. These animals comprised the unclaimed "strays," the incurably wounded or maimed, the vicious and the aged. Healthy but unwanted animals, also, were occasionally destroyed.

As the study of the helminths of dogs and cats seems to have been greatly neglected in Wales, it was decided to carry out the following investigation to ascertain the presence of parasitic helminths, and to deal with any problem or problems arising out of the study.

Since January, 1925, fifty-nine dogs and 155 cats have been examined, and though the investigation is being continued it is thought desirable to publish the data already collected.

The bodies were dissected while warm, and the various organs were carefully examined for parasitic worms. No Trematoda or Acanthocephala were found, and it was noted that the liver was particularly healthy in all animals. Only eleven dogs or 18·6 per cent. were free from infection by parasitic worms. The remaining forty-eight were infected as follows:—*Dipylidium* in twenty-five dogs, *Tenia* in twenty-six, *Multiceps* in two, *Uncinaria* in twenty-two, *Belascaris* in fourteen, and three dogs harboured *Echinococcus*. Of the cats, thirty or 19·3

per cent. were free from worms. The remaining 125 were infected as follows:—*Belascaris* from eighty-four cats, *Dipylidium* from eighty-nine, *Ollulanus* from twenty, *Tania* from seven, and *Capillaria* from one cat. Larvæ and adults of *Ælurostrongylus* were found in thirty cats.

All parasites recorded here by the writer will be deposited in the helminthological collection of the Institute of Agricultural Parasitology, London School of Hygiene and Tropical Medicine.

CESTODA.

TÆNIA HYDATIGENA Pallas, 1766.

This parasite was collected from the small intestines of dogs and cats. It occurred in cats on two occasions and in dogs on eight occasions. Only one was found in each of the cats, whereas eighteen was the largest number obtained from one dog.

Hall (1920) remarks that *T. hydatigena* is reported from *Felis catus* (*F. domestica*) by Stiles and Hassall (1912), but that he has not found the reference in question. For the purposes of his (Hall, 1920) paper the case of this report "will have to be regarded as proven." This present record shows that *T. hydatigena* may be an occasional parasite of the domestic cat.

The larval form, known as *Cysticercus tenuicollis* (the Welsh term, used by butchers is "dwr ci" = dog-water), is often found in the livers, mesenteries and peritoneums of sheep and pigs killed at the municipal slaughterhouse. It may be pointed out that in 1922 the writer obtained this larval cyst from the urinary bladder of a ram, but it was not possible to observe any particular symptoms in the ram, as it was already killed and "dressed" for sale.

TÆNIA PISIFORMIS (Bloch, 1780) Gmelin, 1790.

This, also, was a common parasite occurring in the small intestines of dogs and cats. It was collected from three cats and five dogs. The larva, *Cysticercus pisiformis*, is very abundant in the mesenteries of rabbits of the surrounding country districts.

This parasite, according to Hall (1920) is not a normal feline form,

only "developing to a certain stage at least."

Dramard and Benoit-Bazille (1905) report *T. pisiformis* from *Felis tigris*, and Ackert and Grant (1917) fed kittens with *Cysticercus pisiformis*; only immature *T. pisiformis* of 22 mm. long were developed.

The specimens here recorded (one from each of the two cats) were adult forms, but they must be considered as occasional parasites of the domestic cat.

TÆNIA TÆNIÆFORMIS (Batsch, 1786) Wolffhügel, 1911.

This is not so common as the two previous species; it was found in the small intestine of two cats. The larval stage (*Cysticercus fasciolaris*) of this tapeworm was collected on one occasion from a cyst in the liver of the brown rat (*Epimys norvegicus* Exrl.).

Hall (1920) gives the measurements of the large hooks of this worm as ranging from 380μ to 420μ long. One of the above specimens, from a dog, had the large hooks 437μ long.

MULTICEPS SERIALIS (Gervais, 1847) Stiles and Stevenson, 1905.

A partly disintegrated specimen of this species was obtained from the small intestine of a cat. The disintegration might have been caused by the abnormal situation, for this tapeworm is not a normal parasite of the cat. Cats, in country places, are often seen hunting for rabbits. It is therefore possible that this particular cat became infected with a tapeworm, which developed, but which was later affected by its strange host. The larva, *Cænurus serialis*, has been collected on many occasions from the musculature of rabbits caught at Aberystwyth.

MULTICEPS MULTICEPS (Leske, 1780) Hall, 1910.

The larval form (*Cænurus cerebralis*) of this tapeworm has been collected on many occasions from the brains of sheep killed at the local municipal abattoir. The parasite was collected from two dogs. In one dog forty-two specimens were found, in the other, five specimens.

ECHINOCOCCUS GRANULOSUS (Batsch, 1786) Rudolphi, 1805.

Although the larval stage of this adult parasite is very common in

sheep and pigs killed at the slaughterhouse, it is surprising that on three occasions only did the writer find the adult forms. From the small intestines of a 12-year-old retriever, 206 *E. granulosus* were collected; few from the other two. Walton (1917) and D. O. Morgan (1925) also found the larval echinococcus cyst at Aberystwyth slaughterhouses. It may be of interest to remark that one case of hydatid in human beings occurred at the Cardiganshire Infirmary at Aberystwyth during the period of this investigation.

DIPYLIDIUM Leuckart, 1863.

Very little attention seems to have been paid to the occurrence of the species of this genus in Great Britain. The only species recorded in this country are *D. caninum*, which has been accepted as common, and *D. sexcoronatum* reported by Sondhi (1923) as found in dogs from Birmingham and Leeds. On examining live specimens of *Dipylidium* some slight variations were noted which suggested that more than one or two species were present in the collection. A large number were mounted, stained and carefully examined, with the result that the following species were found in the small intestines of the animals examined.

D. CANINUM (Linnæus, 1758) Railliet, 1892.

In America, Millzner (1926) found that of the specimens examined by her from cats and dogs in California, very few were identified as *D. caninum*.

Sondhi (1923) states that "contrary to expectations" *D. caninum* was not met with in the material from Lahore.

Tubangui (1925) also records this species from the Philippine Islands, but does not remark upon its frequency.

Meggitt (1927) found this species in Burma and remarks that "it is peculiar that dogs and cats in Rangoon and Calcutta (Chandler, 1925) should be infected by this species, while in Nagpur it is rare, and in Lahore (Sondhi, 1923) entirely absent."

This species was not very common among the specimens of *Dipylidium* examined. Out of eighty, only seven were identified as *D. caninum*.

D. SEXCORONATUM von Ratz, 1900.

This species has been recorded as occurring in dogs in England by Sondhi (1923). At Aberystwyth three specimens were collected from cats, and four specimens from dogs.

D. GRACILE Millzner, 1926.

According to Millzner, who formed this species, *D. gracile* is by far the most common Dipylidium of cats and dogs in California.

It is a very common parasite of cats in this district, but up to now it has not been found in dogs.

Occasionally, specimens may be obtained, which when fixed, stained and mounted, present irregular indentations at the margins of the segments, and the neck may sometimes appear to be very small, or even absent. In such cases the specimen may be mistaken, on superficial examination, for *D. sexcoronatum*. The number of rows of hooks and other characters given by Millzner, however, easily distinguishes *D. gracile* from *D. sexcoronatum*. This is the first record of *D. gracile* outside the U.S.A.

D. CRASSUM Millzner, 1926.

This Dipylidium was found in dogs only, but was quite a common parasite. Millzner finds this to be common in the dogs of California.

The specimens of *D. crassum* examined by the writer differ in some respects from those of Millzner. The main differences are that (1) the measurements of the ovary and vitellaria given by Millzner are .545 mm. long by .255 mm. wide and .290 mm. long by .180 mm. wide respectively, whereas those by the writer are .240 mm. long by .288 mm. wide and .192 mm. long by .137 mm. The discrepancy might have arisen out of the method of fixing. Millzner used a camel's hair brush dipped in warm acetic sublimate to straighten the worms and to keep them from contraction. The writer fixed the specimens in alcoholic acetic sublimate and allowed the specimen to straighten by its own weight when held up. Millzner might have stretched the ovary and vitellaria or the specimens of the writer might have contracted; (2) the number of testes given by Millzner is 150 to 175; the writer finds the range from 200 to 250.

D. LONGULUM Millzner, 1926.

Specimens of this tapeworm were collected from the small intestine of cats.

D. WALKERI Sondhi, 1923.

Sondhi described this as a new species of *Dipylidium* found in dogs in the Punjab. Of this species eight specimens have been collected from dogs at Aberystwyth.

On examination of the specimens it was found that there were some differences in the detailed characters of the species obtained by the writer and those of Sondhi. But the measurements of the cirrus when referred to the drawing of a mature segment by Sondhi suggest that Sondhi has probably made an error. The characters as observed by Sondhi and as observed by the writer are given below, but it may be stated that whereas in Sondhi's drawing the cirrus is obviously longer than the diameter of a testis the measurements show that the diameter of a testis is obviously greater than the length of the cirrus.

It has been observed also that the neck may be very short or absent, or it may extend to about .75 mm.

	Sondhi.	Writer.
Hooks	6 to 7 rows	6 to 7 rows.
Rostellum	63 μ to 100 μ at widest portion	Conical, 0.100 mm. at widest portion.
Head	263 μ to 361 μ (rost. invag.); 185 μ (rost. evag.)	0.290 mm. by 0.240 mm. (rost. evag.)
Suckers	118 μ to 150 μ diam.	0.173 mm. by 0.154 mm.
Neck	Short neck	Nil to 0.75 mm.
Mature segment	Length 3 times width	2:1.
Gravid segment...	4.5 mm. to 8 mm. long by 1.5 mm. to 2.5 mm. broad	Same as Sondhi.
Cirrus	45 μ to 54 μ long by 14 μ to 21 μ wide	0.115 mm. long by 0.057 mm. wide.
Testes	Approx. 225	190 to 226.
Diameter of Testis	72 μ to 90 μ by 54 μ to 59 μ ...	0.067 mm.
Eggs	1 to 15 in capsule	1 to 15 in capsule.
Primordia	—	26th to 28th segment.
Ovary	—	0.288 mm. by 0.192 mm.
Vitellaria	—	0.210 mm. by 0.192 mm.
Hooks	Large, 12 μ long; small, 2 μ ...	Large, 12 μ ; small, 2 μ .
Strobila	10 cm. to 28 cm.	10 cm. to 28 cm.

That few testes extend lateral to the longitudinal excretory canals holds in the specimens examined.

NEMATODA.

BELASCARIS MARGINATA (Rud., 1802).

This Nematode was found in the small intestines of seven dogs, or in 16·3 per cent of the dogs examined. The largest number found in one dog was fifteen worms.

BELASCARIS MYSTAX (Zeder, 1800).

This parasite, found in the small intestines of 63 cats, or in 61·8 per cent. of the cats examined, was very much more common than the species found in the dog. The largest number found in one cat was twenty-nine worms.

UNCINARIA STENOCEPHALA (Railliet, 1884).

This parasite occurred in the small intestines of twenty-two dogs, or in 36·3 per cent. of the dogs examined. As many as 194, and 172 worms of this species were found in two dogs respectively. Usually the numbers varied between two and seventy worms in the small intestine.

OLLULANUS TRICUSPIS Leuckart, 1865.

O. tricuspis was collected from the stomach wall of eighteen cats. It was usually present in large numbers embedded in the mucus of the wall. Cobbold (1873), Stirling (1877) and Cameron (1923) have recorded this worm from Britain. Cameron (1926) draws attention to the confusion of the larval form of this worm with that of *Ælurostrongylus abstrusus*, a parasite of the respiratory tract of cats.

ÆLUROSTRONGYLUS ABSTRUSUS (Railliet, 1898).

This was found parasitic in the respiratory tract of thirty cats. Larvæ also were found free in the bronchioles, in the windpipes and also in the tissues of the lung.

CAPILLARIA sp.

From the urinary bladder of one cat, three specimens of *Capillaria* sp. were obtained.

MALFORMATIONS.

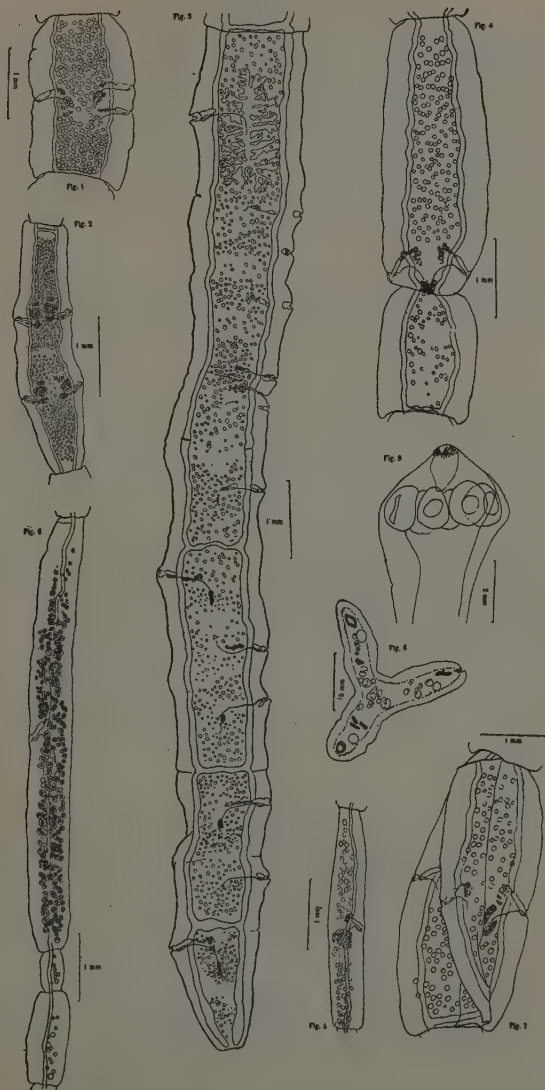
While examining 163 mounted specimens of the cestodes from dogs and cats it was observed that 6 (3·6 per cent.) presented abnormal features or malformations. Malformations, however, are not infrequent in cestodes for they have been recorded and discussed by many early helminthologists.

Leuckart (1886) referring to *Tænia saginata*, states that the multiplication of the genital openings is by no means rare, and that traces of it may be seen in almost every strobila, but that, as a rule, the multiplication is inconspicuous and limited to a few "joints." He also points out that Pallas mentions "joints" with two or three genital openings, and that he (Leuckart) himself had counted five such openings in one "joint," whereas Colin (1876) mentions an unsegmented piece 15 cm. long, which must have possessed at least twenty to thirty genital openings.

In two specimens of *Dipylidium* a malformation shown in fig. 1 was observed. There are three genital pores in a single normal segment. The two genital sets on the one side are not normally developed as is the one set on the other side. The presence of the transverse excretory canal indicates that this "joint" is a normal segment where true multiplication of the genitalia has occurred.

A multiplication as stated by Leuckart arises out of the incomplete separation or individualisation of two segments. Leuckart himself quotes a case of *Tænia cucumerina* where four sets of genital organs occur in one unsegmented portion. Fig. 2 is a drawing of such a case in a *Dipylidium*. The whole "joint" possesses four sets of genital organs, and one transverse excretory canal at the posterior end. The testes, however, are not continuous throughout the length of this "joint." Halfway along the length there is a definite clear space dividing the joint into two groups, each group representing the organs for a normal segment. The "joint" measures twice the length of a normal segment, and but for the absence of a transverse excretory canal in the anterior group, it is clear that this is a case of incomplete individualisation of two segments.

In a *Tænia pisiformis* (fig. 3) an unsegmented "joint" 2·6 cm. long presents a further example of multiplication of genital openings due



Figs. 1, 2, 4, 5, 6, 7, 8 and 9 showing various malformations in *Dipylidium*; fig. 3, malformation in *Taenia pisiformis*.

to incomplete segmentation. The anterior region of this piece possesses a normally developed cirrus pouch, vagina, and uterus. The presence of the uterus shows that fertilisation has taken place. Posteriorly to this uterus there are thirteen genital openings, but the genitalia of these have atrophied with the result that fertilisation and the consequent development of uteri and eggs has not taken place. Indications of segmentation are presented by the presence of three transverse excretory canals, and by incomplete lines of division.

The absence of uteri in the posterior region is interesting in view of the fact that Salzmann (1861) points out, in the case of *Dipylidium*, that fertilisation, and formation of eggs, takes place when the male genitalia are absent on one side of the proglottid; and even the absence of the vas deferens on both sides of a proglottid does not hinder the development of mature eggs in that proglottid. In the case of this *Tænia pisiformis* it shows that where the genital organs are not normally developed, or where they have atrophied, development of mature eggs and uteri does not occur.

Another malformation was noted in a *Dipylidium*, the "joint" of which was longer one side than the other. In this "joint" there were three normally developed sets of genitalia. Two sets occurred in the anterior region, and one set opened by a genital pore on the longer side in the posterior region. Between the anterior sets and the posterior set was a segmenting line reaching to within a third of the width of the segment. Such a malformation is shown and described by Skrjabin (1923).

Malformations may also arise by the complete division of a normal segment. In fig. 4 the normal segment is divided into two portions, the anterior of which has normally developed testes, and two sets of genitalia at its posterior extremity. Immediately posterior to the genitalia a segmenting line occurs which cuts off a portion of the normal segment. This portion possesses the transverse excretory canal which would have normally existed in the one (now divided) segment. The posterior portion is sterile, which indicates that the separation took place before fertilisation. In fig. 6 a somewhat similar segmentation is shown.

Another *Dipylidium* presented a type of malformation (figs. 7, 8

and 9) which involved the whole worm. Küchenmeister (1881) regards this type as a variety since they are determined by a special law of development. The strobila consisted of a series of triangular proglottids (three-rayed in transverse section, fig. 8). For the first mention of this type we are indebted to Bremser (1819). An exact description of the abnormality in his *Tænia saginata* is not given, but from his illustration of it the genital openings occur on one ray or ridge, and an occasional genital opening on another. Levacher (1841) observed a somewhat similar abnormality in *T. saginata*. To such a type belong also the *Tænia lophosoma* of Cobbold (1866), the "Hottentot *Tænia*" described by Küchenmeister and the case mentioned by Cullingworth (1873).

In this specimen of *Dipylidium* it is interesting to note that the genitalia and genital pores occur in each of the rays or ridges. Unlike the *Tæniæ* of the above authors each ridge has normally developed genitalia. The transverse excretory canal of each ridge joins the others in the central common area at the posterior end of each proglottid. The longitudinal excretory canals are normal; eggs and egg-capsules have developed in the gravid segments showing that fertilisation has taken place as in the normal *Dipylidium*. According to Leuckart (1886) this type of malformation in the chain of segments is usually associated with a six-rayed scolex. In this case also the scolex was six-rayed (fig. 9) and bore six suckers and an irregular, but compact, cluster of rostellar hooks.

In another *T. pisiformis*, and one *Dipylidium* a number of proglottids some distance behind a normal scolex showed slight elevations similar to the third ridge of the above triangular forms. This elevation was weakly developed and was restricted to a dozen or so segments, while all the other proglottids of the strobila were normal. This seems to indicate that the triangular type may arise apart from the influence of the six-rayed scolex.

Referring to *Dipylidium*, Salzmann quotes the absence of the male genitalia on one, and on both sides, of two proglottids respectively. It seems that no malformation as is shown in figs. 5 and 6 has yet been recorded. A specimen of *Dipylidium* consisted of a whole series of such abnormal proglottids. Each proglottid possesses only one genital

pore and one set of genitalia. The genitalia on one side are absent. The testes are few in number; there is one longitudinal excretory canal running down the centre of each proglottid and there is an entire absence of transverse excretory canals. Unfortunately the scolex was lost before the specimen was fixed. Fig. 6 shews that the development of eggs and egg-capsules has occurred as in a normal specimen.

ACKNOWLEDGMENTS.

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On the Anatomy of the Vinegar Eelworm.

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INTRODUCTION.

IN the extensive literature devoted to this worm are many anatomical descriptions, the earlier of which are, according to modern standards, vague and superficial. But among recent authors de Man (1910) has given a full and illustrated account with detailed measurements of some forty specimens, an account to which it might seem difficult to add anything of importance. However, the present writer is preparing a paper on the bionomics of the worm, and therefore considers a brief anatomical description to be desirable, particularly as de Man's paper may not be easily accessible to those interested.

This paper, then, contains an account of the structure of the adult worm, based on the writer's observations. Notes on reproduction and life-history are added; marked variations in the size and structure of the worm are discussed, and finally the relationships of the worm to other species of the genus are briefly considered.

It may be mentioned here that the writer (1927) has produced evidence to show that, according to modern procedure in nomenclature, the old name of the genus, *Anguillula*, is not valid: he has proposed instead the name *Turbatrix*, with *T. acetii* (the vinegar eelworm) as type species.

The writer wishes to express his indebtedness to Professor R. T. Leiper for making accessible much valuable literature and for placing at his disposal a culture of the worms, and to Dr. J. N. Oldham for a second culture.

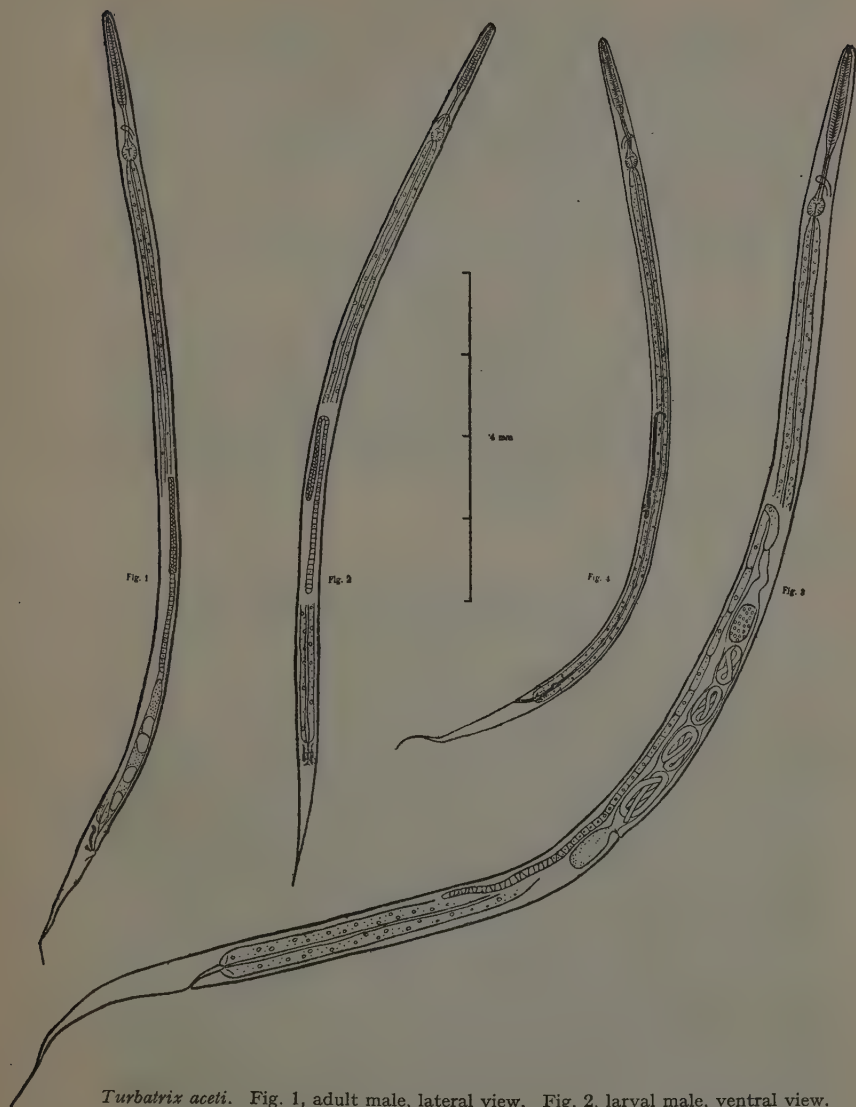
THE ADULT STRUCTURE.

If a sample of infested vinegar is held up to a bright light, the eelworms are to be seen by the naked eye, mostly at the surface of the vinegar, rapidly and incessantly moving. When killed by heat they straighten out, except for a ventral flexure of the posterior end of the body which is much more marked in the male. It is then seen that the fully grown females are about 2 mm. long and 0.05 mm. broad, while the males are about 1.4 mm. long and 0.03 mm. broad. The worms are truly cylindrical throughout the greater part of the body. The anterior region narrows slightly from about the level of the œsophageal bulb and ends in a rounded head perforated by a small terminal mouth, while the long tail gradually tapers off to end in a fine point. Seen under a 1/12 in. oil-immersion lens, the cuticle presents very fine transverse striations.

Although the cuticle is transparent, it is difficult to see much of the internal structure owing to the presence of numerous refractive globules which are apparently reserve food substances. These are fairly plentiful in the œsophageal region, but attain their maximum concentration abruptly at the beginning of the intestine, which they surround: from here they become gradually smaller and less numerous until in the tail region they are practically absent. For the sake of clearness they have been totally omitted from the accompanying drawings, but it should be understood that the latter bear little resemblance beyond similarity of outline to the actual picture presented by the worm under a microscope: a superficial glance usually reveals nothing but globules. Further details as to the nature of these bodies will be added later.

The small mouth-pore leads into a narrow buccal cavity, about 0.01 mm. long, in the form of an inverted truncated cone, and more extensively cuticularized on the dorsal side. The posterior half of this cone is embedded in the anterior end of the œsophagus and bears three minute teeth—two ventro-lateral in position, and the stouter third dorsal. A ring of six papillæ surrounding the mouth is figured by de Man, but the writer has not succeeded in getting a frontal view of the worm.

The œsophagus consists of an anterior slightly conical portion about 0.014 mm. in mean width and 0.1 mm. long, succeeded by a narrow neck 0.005 mm. wide and half the length of the anterior portion, which leads in turn into the muscular bulb. There is no trace of the supporting



Turbatrrix aceti. Fig. 1, adult male, lateral view. Fig. 2, larval male, ventral view.
Fig. 3, adult female, lateral view. Fig. 4, larval female, lateral view.

laminæ which Goodey (1922) has observed in the substance of the anterior portion and neck of the œsophagus of the paste eelworm. The bulb is roughly spherical, about 0.02 mm. in diameter, and contains a typical valvular apparatus. It is almost impossible to distinguish the excretory pore (de Man does not figure it at all): out of some dozens of specimens examined, the writer found it definitely in one case only—at the level of the anterior end of the bulb.

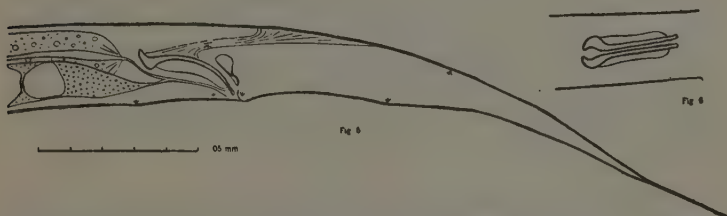
The nerve-ring sweeps forwards and upwards and crosses the œsophageal neck at about 0.014 mm. in front of the bulb.

The intestine, about 0.02 mm. wide in the female—proportionately narrower in the male, runs straight back to within a short distance of the anus to which it is connected by a narrow rectum; in the adult female it is compressed and pushed dorsally in the region of the uterus. The lumen was found to be very narrow in most of the worms examined, though in some specimens it fluctuated markedly in width along the gut—an appearance to be noted again later.

Male Reproductive System.

In a male worm 1.2 mm. in length (fig. 1) the testicular tubule arises ventrally at about 0.3 mm. from the ano-genital pore. In all specimens examined it passes forwards for a distance of about 0.1 mm., then turns abruptly and runs back towards the ano-genital pore. This flexure of the gonad always lies in a horizontal plane, so that when the worm is lying on its side (as it naturally tends to do) the point of origin of the gonad is difficult to distinguish without careful focusing. If the preparation has been suitably stained, however, it will be seen that the first portion of the gonad consists of cells in two or three rows, while in the region of the bend it becomes a single row. If the worm can be rolled over to present its ventral or dorsal surface, the bend and the change in the arrangement of the cells will readily be seen (fig. 2). This rachis of single cells extends backwards from the bend to about twice the length of the first portion, after which it ends abruptly. There follows a thin-walled, irregularly wider vesicula seminalis, which tapers posteriorly until it joins the rectum to form a short narrow cloaca. Masses of sperm cells are visible in the vesicula, but these are usually separated by large clear vacuoles.

According to Poupin (1898) there are *paired testes* in the male ("El aparato jénital masculino nace . . . por dos cordones . . . situados lateralmente; . . . estos constituyen los testículos . . ."). This is certainly not the case in the worms examined by de Man and by the present writer. Possibly Poupin viewed the males only from a lateral aspect (they invariably lie in this position on the slide by reason of the flexed tail), and saw in distinct focal planes the two superimposed sections of the single tubule: a ventral view would have shown him that the sections are connected anteriorly.



Turbatrix aceti, posterior region of male. Fig. 5, lateral view to show spicules, accessory piece and papillæ. Fig. 6, ventral view of spicules only.

There is a pair of similar spicules the heads of which are broader than the shafts and are flexed dorsally, giving the whole spicule a slight S-shape. Attached to them ventrally along almost the whole length are thin transparent laminæ, of which only the ventral edges, towards the middle of their length, can be seen at all clearly. These laminæ extend outwards ventro-laterally, since they are also visible from a ventral aspect. According to de Man they subsequently curve inwards ventrally and overlap, so forming with the spicule shafts a more or less completely closed tube which serves as a seminal duct in copulation.

The accessory piece, which is simple in construction, takes the form of a slightly curved plate, thickened at its ventral end, and bears posteriorly a very thin lamina which lies in the median vertical plane and which is not very constant in outline. The entire accessory piece may be said to resemble the keel of a boat bearing a deep keel-plate.

The spicules are very constant in size and shape, being 0.037 mm. long as measured along the dorsal curve from tip to tip, and about 0.033 mm. long as measured directly. The accessory piece is about 0.012 mm. long. The extensor muscles of the spicules are usually clearly visible, each attached at one end to the head of the spicule and at the other to the dorsal body-wall of the worm; the keel-plate of the accessory piece often lies between these two muscles.

Five pairs of papillæ are present. Of the four ventral pairs two are pre-anal, one ad-anal and one post-anal, their respective distances from the ano-genital pore being about: 1st, 0.033 mm.; 2nd, 0.008 mm.; 3rd, immediately behind the pore on the prominent posterior lip, and 4th, 0.046 mm. The fifth pair is post-anal and dorsal, at about 0.066 mm. from a point immediately opposite the pore. The first and fourth pairs are fairly easy to see, particularly in a dead and macerating specimen: the other three pairs are usually visible only with the high powers of the microscope.

Female Reproductive System.

The position of the vulva divides the body-length in the approximate proportions of 12:10. From it runs forwards ventrally the anterior uterus, for a distance of about 0.4 mm., when it turns back on itself and narrows to meet the ovarian tubule. The latter runs back dorsally, usually to some distance posterior to the vulva. From the vulva, and opposite the anterior uterus, runs back a short blind oval sac the dimensions of which vary considerably around a length of 0.07 mm. and a breadth of 0.015 mm. This sac (which de Man calls the "ovarium") probably serves as a receptaculum seminis, and is thought to be the homologue of the posterior ovarian tubule and uterus, which are otherwise absent in this worm. The ovarian tubule is seen to consist of a rachis of cells in single series. These cells are small at first, but more proximally they elongate without increasing in width until they reach the anterior flexure of the tubule. At this point they break off from the rachis and assume an oval shape and size very similar to the shape and size of the ovarium. Here, segmentation of the ova is first observed, so that fertilization must occur at this point. The number of embryos in the uterus varies considerably (see below) but two ovoid and three vermiform embryos may be taken as typical. The embryos appear to be enclosed in a

very thin egg-membrane but, according to the writer's observations, this breaks before the young are born : thus the vinegar eelworm is viviparous. The vagina is without any marked musculature such as is found in *T. rediviva* (*vide* Goodey) and in *T. ludwigii* (*vide* de Man).

The Reserve Food-Substances.

Bastian (1865) notes that the anatomical features of the vinegar eelworm are "much obscured by colourless granules within the integument." Henneberg (1900) also refers to "round globules which are found in large numbers in well-fed worms" and considers them to be of a fatty nature. At the time when the present work was being done, Dr. T. Goodey was investigating the chemical nature of reserve food-substances in certain other nematodes, and was testing for the presence of fats by staining the worms with Scharlach R and Nile Blue : to him the writer is indebted for the suggestion of this technique. Of the two stains mentioned, Nile Blue is without effect on living worms, while Scharlach R stains them considerably. The best results, however, are obtained when the worms are first killed in hot 70 per cent. alcohol or in Ditlevson's fixative, and are then subjected to alcoholic solutions of Scharlach R or of Nile Blue sulphate. After this treatment, in the case of Scharlach R, the globules are all stained a bright red, the rest of the worm remaining colourless or being tinged very faintly yellow. In the case of Nile Blue the globules are stained red while the remainder of the worm is stained blue to varying degrees—according to the tissue affected. The blue stain may tend to obscure the colour of the globules, but if the worm is crushed under a cover-glass the globules escape from the body and run together, and the red colour is then distinctly seen. The reactions of both these stains indicate that the globules are of a fatty nature. Lee ("The Microtomist's Vade-mecum") quotes Lorrain Smith (1907, *Journ. Path. Bact.*, XII, p. 1) to the effect that Nile Blue stains fatty acids blue and neutral fats reddish, in which case the globules in the vinegar eelworm are composed of neutral fats. Minute fat-globules can be distinguished, using Scharlach R, within the body of embryos *in utero*, which suggests that they are derived from the ovum. The latter has never been found to stain with Scharlach R, however ; possibly the neutral fats are synthesized by the embryo from other chemical substances contained in the ovum. In describing similar globules in the free-living eelworm *Rhabditis monhystrera*, Conte

(1900a) notes that they often invest the uterus, particularly when the worm is living in a poor medium and the globules have disappeared from other parts of the body. The writer has never found fat-globules intimately associated with the uterus in the vinegar eel: their distribution is always the one already described above; though they certainly become less numerous in worms that are living in an exhausted medium. In view of this latter fact, and of the difficulty experienced in making out the internal structure through the compact layer of globules, the suggestion has been made that the worms should be starved for some weeks before an anatomical examination is attempted: under these conditions the fat-globules are greatly reduced in number so that they are less likely to obscure the structure. The writer is strongly opposed to this procedure, for reasons which will be apparent later.

Quite apart from the demonstration of fat, the use of Nile Blue as a stain can be recommended (in this worm at least) on account of the tissues which are stained blue. These are the cesophagus, the entire reproductive system of both sexes—including the male spicules, and certain cells of the intestine. In this way, the development of the reproductive system in particular has been observed by the writer; this and the distribution of the intestinal cells mentioned will be described in the following section.

LIFE-HISTORY.

The vinegar eelworm lives through its entire life-cycle in vinegar under normal conditions, and this may be said to comprise its life-history in the strict sense of the term. But the term is used here more loosely to include the embryology and the larval development; under it are also included some interesting data on reproduction which are due to Henneberg.

Reproduction.

Henneberg has found that male and female worms are normally present in a culture in approximately equal numbers. The young larvæ attain sexual maturity in about four weeks, after which the females are, usually, continuously pregnant. The greatest number of young observed to have been produced by a single isolated female was 45. A fertilized egg reaches maturity and is hatched in about eight days. One

worm was found to reach an age of ten months. Frequently a female dies before all the developing embryos are hatched ; in this case development continues, the embryo hatches *in utero* and crawls about within the body of its mother (the writer has often seen the tail of a dead female being moved to and fro by the agency of a larva imprisoned within it). In one case Henneberg found that two larvæ lived for 22 days in such confinement. Under favourable conditions propagation is very rapid : in vinegar to which a single female had been added there were " innumerable multitudes of worms after seven months." Sixty-eight descendants of a single worm were to be counted by the end of 24 days.

Embryology.

The passage of the unfertilized ova along the ovarian tubule until they break free into the uterus has already been described. Two-cell and four-cell stages of segmentation can frequently be discerned *in situ* without difficulty.

A remarkably full account of the embryology of this worm was given by Hallez (1876). He chopped up a number of worms with a scalpel and added a drop of water ; in this way many eggs were liberated and the required stage of development could be selected. He found that ammonia-carmin was a suitable stain, being preferable to picro-carmin in that the obscuration of the pink cell-nuclei by the yellow colour of the protoplasm was avoided.

Hallez stated that deutoplasm and a vitelline membrane were absent ; the embryo appeared to be nourished at the expense of the albuminous fluid within the matrix. Segmentation gives rise to a morula which hollows out to form a blastula. At the blastular stage can be distinguished a pair of adjacent larger cells at one pole : these cells determine the orientation of the embryo and mark the future anterior end. At the opposite pole is a single cell similarly distinguished on account of its size. Invagination of the blastula commences equatorially (between these two poles) and results in a typical gastrula, the blastopore of which narrows and finally closes. Hallez is emphatic about this, for Bütschli, working on *Cucullanus elegans*, had apparently derived the final mouth from the blastopore ; Hallez shows that the latter occurs in the region of the future tail. The blastocoele is obliterated after gastrulation, but

the endoderm and ectoderm may separate under the influence of the fixative. The archenteron produced by gastrulation persists as the final gut. The two anterior cells sink beneath the ectoderm (to which they largely give rise) and by rapid proliferation form a sheet of mesoderm in the anterior region. This sheet gradually spreads backwards between ectoderm and endoderm. Before it has spread far, an invagination at the site of the original anterior cells gives rise to the stomodæum, which persists as the true mouth. During these processes the posterior region of the embryo elongates considerably to form a narrow tail, the whole embryo now resembling a tadpole.

It is remarkable to find such detailed work on the embryology of a nematode appearing some years before Zur Strassen's classical paper on the development of *Ascaris megalocephala*. It is impossible to say at present how reliable Hallez' description may be, but it bears marked similarities to the ascertained development of *Ascaris*.

In the literature are many references to the worms being oviparous, which is certainly not the case in the worms examined by de Man, by Henneberg, or by the present writer. Henneberg states that unfertilized or undeveloped eggs may occasionally be deposited, and suggests that the above misconception may have originated in this fact. The writer has frequently seen an unsegmented ovum close to the vagina, with fully developed vermiform embryos distal to it; this abnormal condition is fairly common in an old or putrescent culture.

Larval Stages.

The occurrence of definite larval stages, each terminated by a moult, is difficult to establish owing to the fact that there are no marked or sudden changes in any of the structures: all that can be said is that moulted skins are occasionally to be found. This fact was recorded as early as 1773 by O. F. Müller, whose interesting observation may be roughly translated: "I suspect that the worms shed their coats; indeed, I have seen specimens the anterior and posterior part of which was enveloped by a projecting hyaline membrane resembling a sheath."

The newly born larva is about 0.2 mm. long, and already contains a number of fat-globules. The entire alimentary system is a miniature facsimile of that of the adult. The genital rudiment is represented by

a single cell occurring at about the mid-length of the body and ventrally. This may be difficult to see in the natural state, but after staining with Nile Blue it is made obvious as a dark blue spot. The sexes are not distinguishable at this early stage.

While the writer was examining slightly older larvæ, certain darkly staining cells were seen embedded in the intestine with their inner faces abutting on the lumen. From the lateral aspect they appeared to occur in pairs, roughly opposite each other ; but since a similar appearance was given from a ventral aspect it seems probable that what was taken for a pair is actually a ring surrounding the lumen. They are more distinct in the posterior part of the gut, and are fairly constant in distribution. There are normally three such rings, evenly spaced, between the rectum and the region of the genital rudiment, and two more are sometimes discernible further forwards. Five rings are shown in fig. 4, where they appear as small black crescentic bodies bordering on the lumen of the gut. Their nature and function are unknown—possibly they are glandular. The lumen of the gut is normally narrow and of even width, but in worms from stale cultures it is often seen to be successively distended and contracted like a series of hour-glasses. In such cases it has been noticed that the region of maximum distension usually coincides with the position of these rings. Subsequent observation has shown that the rings are also present in adult worms, of both sexes, though they are less easily seen than in larvæ.

In the male larva the genital rudiment proliferates anteriorly to form a rachis of cells which, after growing forward for about 0.1 mm., turns back on itself and extends posteriorly—the flexure lying in the horizontal plane. At the same time a confused mass of darkly-staining cells arises in the region of the rectum and chiefly dorsal to it. Subsequently the primordia of the spicules can be distinguished as (from the ventral aspect) two straight bars. At this stage, which is illustrated in fig. 2, the testicular tubule has almost reach adult proportions. The writer has attempted to discover how the vesicula seminalis arises, but without definite success : in some specimens there is a suggestion that it grows forwards from the cloaca. In the specimen figured there was no clear sign of it. Accordingly, the question as to how the two sections of the reproductive system finally meet remains unsettled.

In the female also, the genital rudiment proliferates forwards, for a somewhat greater distance than in the male, when it turns on itself and grows backwards. The flexure in this case lies in a roughly vertical plane, the tubule crossing over to the dorsal side of the body. At the stage at which the tubule begins to turn (fig. 4) the vagina is clearly visible, in the position of the original rudiment, as a wide short column running down to the body-wall: a slit-like lumen can be distinguished, but there is no communication with the exterior. The ovarium is represented at this stage by a small cluster of cells just posterior to the vagina. Shortly after this the vulva is formed, the dorsal part of the tubule extends further back, and the ventral part acquires a lumen and enlarges to form the uterus.

From a comparison of the development of the reproductive systems in the two sexes it is seen that the male system commences to develop at the distal end (*i.e.*, at what will become the free end of the testicular tubule), while the female system commences to develop at the proximal end (at what will become the vagina).

VARIATIONS IN SIZE AND STRUCTURE.

In his description of the vinegar eelworm Bastian (1865) noted that the size of the female was very variable. The writer also has noticed this, in worms from a single culture, but the reason seems to be that the female worm becomes sexually mature before it has reached its maximum size. It is important, therefore, to select the larger mature females for the purpose of making measurements.

Henneberg noted that in cultures where the food was insufficient the larvæ remained small, and did not attain sexual maturity even after living for ten months (it is normally attained in about four weeks). He also stated that the size of the adult worm varied according to the nature of the culture medium. Thus smaller forms appeared in vinegar made by the Rapid Process than in wine-vinegar or in media with an extensive bacterial flora or rich in organic matter. The worms became shorter and broader when cultured in an acidified barley-malt medium. He also noted that "the worms of a single population vary slightly in the shape of the œsophagus and that of the tail."

Most remarkable variations were recorded by de Man, who described forms from two samples of vinegar. Both samples were of spirit-vinegar

(made by the Rapid Process) and in both, eelworms were abundant ; but in one, the mature adults were only half the size of those in the other. Some of the actual measurements for these two forms will be given below.

In the matter of structure, only slight variations have been recorded in the literature for the relative proportions of the digestive system and of the male reproductive system : regarding the latter, the spicules and genital papillæ seem to be very constant in size, shape and position. But the writer has noted marked variations in the female reproductive system, variations which seem to depend partly on the nature of the medium in which the worms are living ; the putrefaction of albuminous media is especially productive of them.

Thus the ovary varies considerably in size and shape. In some cases it is almost spherical, in others it is long and cylindrical, in others again it presents extreme irregularities of outline. In size it varies, independently of its shape, from a structure less than half the body-diameter in width to a structure that almost fills the body-cavity. If the ovary really is a receptaculum seminis some variation in *size* would be expected, and this is actually found in worms from a single fresh culture ; but in these cases the shape remains reasonably constant and resembles that illustrated in fig. 3. But in worms from stale cultures the gross irregularities of *shape* are to be found.

The most marked variations in the female, however, occur in the size, shape and contents of the uterus and of the ovarian tubule. In fresh cultures the general arrangement is that already described and figured. There may be variations in the length of the uterus and of the ovarian tubule, and also in the actual and relative numbers of ovoid and vermiform embryos present. Thus a young female will produce embryos when the ovarian tubule is only half the length of the uterus, and the latter will contain two or three ovoid, and as many vermiform embryos ; while in a fully grown female the ovarian tubule may extend for a considerable distance posterior to the ovary, and the uterus will contain only one or two ovoid embryos and from four to six vermiform embryos (two exceptionally large females contained eight ovoid and two vermiform, and five ovoid and four vermiform embryos respectively, but an excess of ovoid over vermiform stages is very unusual, especially in fully grown forms). Here again, these variations seem to depend merely on the relative ages

of the worms. But in females from putrescent cultures and in those that have been starved, the reproductive system becomes considerably abnormal. The ovarian tubule often zig-zags across the body instead of running straight back dorsally, and instead of being of even diameter it may be grotesquely lobulated in an irregular manner—the ova taking the form of spheres here and there in the place of the usual elongated cylinders. In such worms the uterus often contains only one embryo, or there may be an unsegmented ovum next the vagina with a vermiform embryo distal to it. These worms are always reduced in size, and the reproductive system may be very short, even relatively to the size of the worm.

Conte has shown how greatly the size and structure of *Rhabditis monohystera* are influenced by the nature of the medium in which the worms are cultured. He also found, both with this worm and with *Diplogaster longicauda*, that the females could be made viviparous or markedly oviparous (e.g., eggs were laid in the two-cell stage) simply by changing the culture-medium. The writer has never found oviparous vinegar eelworms but in the older literature there are persistent references to free eggs. In any case it does seem that the size and structural proportions of the worm can be strongly influenced by the nature of the medium. This question will be more fully discussed from the biological aspect in a subsequent paper on the bionomics of the vinegar eelworm; but it is suggested here that dimensions and proportions of all but the most rigid structures may be of doubtful validity for systematic purposes. In some cases it appears that statistical methods will have to be employed, involving coefficients of variation. Only when the dimensions and proportions of two forms are distinctly beyond the limits of variation can they be safely used as diagnostic features to separate the forms.

It will now be clear why exception was taken to the method of starving worms in order to remove the fat-globules and so to render the internal structure more clearly visible. Starvation has a marked influence on certain structures, in the case of this worm at least, so that the anatomy under these conditions is not typical.

Variations in size and in general proportions will be better appreciated if some actual values are given. For this purpose measurements have been collected from various authors and are tabulated below. In the matter of size, the total length and mid-breadth of the worms have alone

been selected: variations in other dimensions are equally striking, but sufficient data other than those of de Man have not been published, and not even in de Man are there values for the over-all length of the female reproductive system. In the matter of proportions, de Man's conventional ratios (α , β , γ ,) have been used, and have been calculated from the data of other authors wherever possible. These ratios are explained by de Man in a footnote (*op. cit.* p. 364) which reads: "For the sake of brevity the ratio of the total length to the mid-breadth of the body will be denoted by α , the ratio of the total length to the length of the œsophagus (in which the mouth is included) by β , and the ratio of the total length to the length of the tail by γ ." The measurements are those given in the texts of the various authors except in the case of Hogg where, since he gives no measurements, they have been calculated from his figures. Opposite the heading "de Man" are two sets of values marked "A" and "B": these are the values for the two forms described from the two samples of spirit-vinegar. Values for *Turbatrix aceti*, var. *dryophila*, from de Man, are added here for convenience and will be discussed in the final section.

Table of Dimensions and Ratios.

(For explanation see text; dimensions are in millimetres.)

<i>Turbatrix aceti</i> , var. <i>aceti</i> .		FEMALES					MALES				
Author	Date	Length	Breadth	α	β	γ	Length	Breadth	α	β	γ
Dujardin ...	1845	1.46	0.032	46	—	—	0.85	0.027	31	—	6.5
Hogg ...	1863	—	—	—	—	—	1.03	0.027	45	6.0	5.3
Bastian ...	1865	1.96	0.046	43	8.9	6.3	1.21	0.03	40	7.0	6.3
Lindner ...	1889	1.5— 2.5	—	—	—	—	1.0— 1.5	—	—	—	—
Poupin ...	1898	2.72	0.064	42	—	—	2.08	0.048	43	—	—
de Man, A. ¹	1910	1.74— 2.43	0.042— 0.053	43— 55	9.0— 10.0	6.2— 7.6	1.5— 1.81	0.026— 0.034	50— 60	7.0— 8.5	7.2— 8.4
de Man, B. ²	1910	0.96— 1.07	0.022— 0.03	35— 40	5.4— 6.0	4.8— 5.5	0.87— 1.0	0.021— 0.025	40— 42	5.0— 5.2	6.0—
Writer's ...		1.4— 2.3	0.03— 0.06	33— 58	8.2— 11.5	6.1— 7.9	1.2— 1.6	0.025— 0.032	43— 53	7.4— 8.3	6.6— 9.7

Turbatrix aceti, var. *dryophila*.

de Man ⁴ ...	1910	0.96— 1.36	0.029— 0.045	27— 40	6.5— 7.1	3.4— 5.3	0.8— 1.1	0.023— 0.032	29— 45	5.4— 6.3	4.4— 5.7
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Based on: ¹ 14 ♀, 12 ♂; ² 11 ♀, 4 ♂; ³ 12 ♀, 10 ♂; ⁴ 23 ♀, 16 ♂, respectively.

Neglecting the values for the variety *dryophila*, it will be seen that there are marked variations, both in the size and in the proportions of both male and female worms. In the case of the females a considerable variation in size would be expected, since they become sexually mature before they are fully grown, and the presence of embryos *in utero* is the only valid criterion in selecting adults. But this fact of itself is insufficient to explain such extreme variations in size as are found in de Man's two populations. In the case of the males the writer has taken the presence of fully formed spicules as the criterion of selection ; that this is justifiable will be seen from his values in the table, where variations in size and in the ratios α and β are much less marked than in the case of the females : the males evidently reach their maximum size soon after sexual maturity is attained. But even when allowances are made for relative age, there remain considerable variations, and these suggest that specific differentiation cannot be based on minutiae, as it has been in the past. Thus Bastian considered that Hogg's figures were those of a distinct species which differed in several respects, " more especially as regards the male spicules," from the true vinegar eel. Hogg's drawings are on too small a scale ($\times 150$) for the details of the spicules to be made out, but in their size and general form they are not markedly different from those figured by Bastian himself (drawn to the same scale) ; and, except for a rather longer tail in Hogg's forms, the general dimensions and ratios are well within the limits of variation. Then again, Leidy (1870) claimed that the eelworm occurring in cider-vinegar in America was a distinct species from the eelworm in wine-vinegar, as described by Bastian, since the oesophagus in the former was rather more like that in *Cephalobus*. The table will show that in Bastian's vinegar eels the oesophagus was somewhat long relative to the length of the body, and in his drawings it is rather wider than in those of de Man and of the present writer ; but here again it must be insisted that the dimensions and proportions are within the limits of variation.

In view of the above discussion, it will be opportune to consider briefly the relationships of the vinegar eelworm to other forms included in the genus.

RELATIONSHIPS.

The old genus *Anguillula* was in the nature of a repository for almost any species of free-living nematode that might be discovered. The task of deciding how many of these species must be included in the new genus *Turbatrix* will be a heavy one. Provisionally, the writer has included in it the vinegar eelworm (type) and a variety, *dryophila*, of the same species (from the white slime-flux of the oak), the paste eelworm, and two new species of de Man's, *ludwigii* and *silusiae*.

The vinegar and paste eels have been considered alternately as one and as two species respectively, ever since Linnæus included both in the species *Chaos redivivum*, in the 12th edition of the "Systema." The earlier stages of this problem have been dealt with from the standpoint of nomenclature in the writer's previous paper. The earlier observers cannot be expected to have made out the minute anatomical details which are of systematic importance, but it is extraordinary to find later workers, optically well equipped, in violent disagreement over the question. Thus Hogg, who noted the S-shaped spicules of the vinegar eel, stated that the paste eel was precisely similar to the vinegar eel, and "Although authors still persist in describing it as distinct, it is nevertheless exactly the same in every particular": yet the spicules of the paste eel are not S-shaped at all. Then Schneider (1866), who considered them as one species, attempted to solve the problem by saying that it was clear that the worm could live in the two media (vinegar and paste). "If one pours a little vinegar into paste, a richly populated colony of vigorous individuals is soon obtained." His drawings are of the vinegar eelworm. But in this matter Henneberg was more cautious, and rightly pointed out that the identity of the two forms was not established by the mere fact that the vinegar eel could live in paste.

Actually the two worms are quite different, as Goodey was able to show in 1922. In the paste eel the male spicules are arcuate, the genital papillæ are differently distributed, and in the female the vagina is strongly muscularized. Moreover, the worms are much stouter, the value for the ratio α being 20, which is well beyond the variation-limits of that ratio in the vinegar eel. Schneider's experiment, however, proves to be the clue to the former confusion, since the old recipe for producing paste eels was to acidify the paste with a little vinegar!

Turbatrix ludwigii (de Man, 1910) and *T. silusiae* (de Man, 1913) are much more similar to the paste eel than to the vinegar eel, with which latter there is no possibility of confusing them. The differentiation of *T. aceti* var. *dryophila* from the true vinegar eel (var. *aceti*), however, rests on less definite grounds. Thus, of the male spicules and genital papillæ, which are usually of such diagnostic importance, de Man says: "As concerns the size and arrangement of the five pairs of papillæ on the male tail, the eelworm from the slime-flux is identical with the vinegar eel; moreover, the spicules and the accessory piece appear to have the same size and shape in both" (he is referring to the B-population of vinegar eels). An examination of the table will show that the variety *dryophila* is of about the same length as the vinegar eels of the B-population. Nevertheless the tail is distinctly shorter in the male of the latter, and the œsophagus longer in the female. These maximum and minimum data conceal some points that appear only when individual data are examined. This latter procedure reveals that, in the males of the two forms mentioned, the tail is longer than the œsophagus in the variety *dryophila*, but shorter than the œsophagus in the vinegar eel (B-population); this does not always apply in the case of the A-population). From the table also emerges the fact that both dimensions and ratios are far more variable in the variety *dryophila* than in the variety *aceti*. In so far as generalizations are possible, it may be said that the tail is relatively long in both sexes of the variety *dryophila*, while in the females the reproductive system has not shortened to the same extent as the body as a whole, with the result that its anterior flexure is relatively near the œsophagus and the posterior end of the ovarium (which is longer than in the *normal* vinegar eel) is relatively near the anus.

The relationship between these two forms is clearly very close. There seem to be no absolutely reliable characters on which to make a specific differentiation. Yet, if the ratios in *dryophila* are compared with those in *aceti* which have been recorded up to date, the two forms can be distinguished. Should vinegar eels be discovered which are intermediate (as regards their ratios) between *dryophila* and de Man's B-population of *aceti*, it would become necessary to unite the former with the latter: such a discovery does not seem at all impossible. Meanwhile, the best course seems to be to leave them as distinct varieties.

SUMMARY.

(1) The anatomy of the adults of *Turbatrix aceti* is described, attention being paid to the distribution and nature of the extensive reserve food-substances, which are shown to be fats. The use of Nile Blue as a specific stain for the reproductive systems is noted.

(2) Data on reproduction are quoted from Henneberg (1900) and on embryology from Hallez (1876). The writer's observations on the development of the reproductive systems in the larvæ are given, and certain intestinal cells of doubtful function are described.

(3) Remarkable variations in size, proportions and structure are collected from the observations of previous writers and of the present writer: it is shown that these variations depend partly upon the nature of the culture-medium.

(4) Of the other worms recently included in the genus by the writer (1927), it is shown that only *T. aceti* var. *dryophila* is likely to be confused with the true vinegar eel. After considering the relevant dimensions and ratios, with their variations, it is concluded that the status of this variety can be maintained provisionally.

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On the Nematode Genus *Aphelenchus*.

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INTRODUCTION.

IT is well known that free-living nematodes are of frequent occurrence in various kinds of rotting organic materials both animal and vegetable under natural conditions. In a recent investigation of the nematodes occurring in a variety of substances such as pig-manure, sheep droppings taken from pastures, soil from a chicken run, decaying leaves from a drain, etc., the writer has made use of the Baermann method (Cort and others 1922) with a good deal of success. Amongst several interesting forms obtained from samples taken from a heap of pig-manure were six worms, four females and two males, belonging to the genus *Aphelenchus*, which at once attracted attention by reason of certain peculiarities in their appearance. They closely resemble *Aphelenchus tenuicaudatus* de Man (1895) in certain anatomical features, but differ on certain points, and the writer regards them as belonging to a hitherto undescribed species.

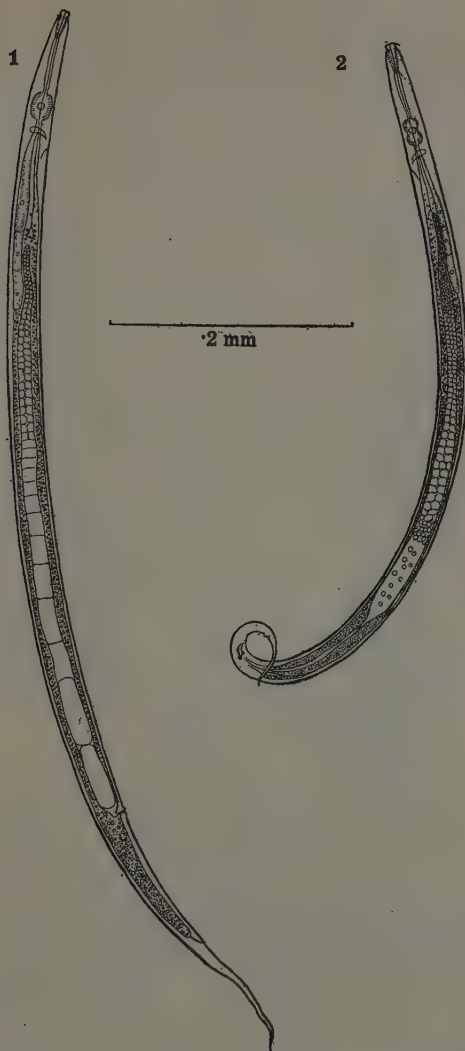
The opportunity is also taken in this paper for a re-description of the type species of the genus *Aphelenchus*, namely *Aphelenchus avenæ* Bastian 1865, at present rather imperfectly known, and for the discussion of the systematic relationships of certain nearly related forms. The various species of the genus will also be briefly dealt with in Part (3) of this paper.

(1) *Aphelenchus winchesi* n. sp. from Pig-manure.*Morphology.*

As figs. 1 and 2 show the worms of both sexes have the shape usually found in members of this genus, *i.e.*, the body tapers before and behind. The tail of the female is long and is drawn out to a fine point as in *A. tenuicaudatus* and *A. helophilus*, and also in the male there is a fairly long tapering tail. The cuticle has fine transverse striations and the head end is distinctly knobbed and separated from the body by a slight constriction. Its sides are smooth and rounded, and only the faintest suggestion of distinct lips is discernible even under the oil-immersion. This absence of well-marked lips is a point of difference from *A. tenuicaudatus* which, as de Man's figures show, has six distinct ones.

Perhaps the most striking feature of the anatomy is the mouth stylet, which is very long and is without basal swellings. In this last respect it resembles the stylet of *A. avenæ* and *A. tenuicaudatus*, in both of which there are no posterior swellings. Its length of 0.025 mm. to 0.027 mm. is the same as that of *A. tenuicaudatus*. In the largest female specimen which was examined alive the stylet was being exerted and withdrawn whilst under observation and one was thus enabled to see its great length and the shape of the tip. The orifice is not at the extreme end but just behind on the ventral side, reminding one somewhat of the buccal apparatus in members of the genus *Dorylaimus*. There appear to be two transverse guides about halfway down its length. A compact system of muscles extends from the constriction just behind the head to the base of the stylet and no doubt serve to protrude the latter.

The lumen of the stylet is continued posteriorly into the first part of the oesophagus, which is rather narrow and extends as far as the muscular bulb. This is a comparatively large structure with stout walls in which the radiating muscles are easily seen. Its shape varies somewhat, being oval in two, more or less cylindroid in three, whilst in one of the males the two sides are pinched in, giving it the appearance of a figure 8. The cuticular lining of the lumen expands outwards at the centre in three crescentic thickenings, which are sharply defined



Aphelenchus winchesi n. sp.

Figs. 1 and 2.—Female and male under low magnification showing shape and principal anatomical features.

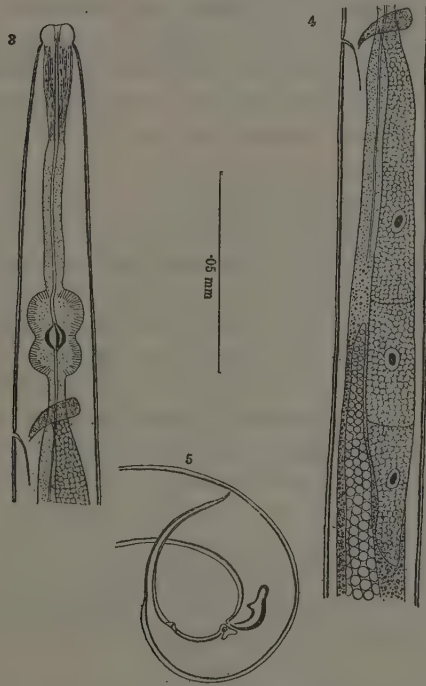
and help to give the bulb its prominent appearance even under low power magnification. Succeeding the bulb there is a short portion of œsophagus of about the same width as that immediately preceding it and here the nerve-ring is found.

The accurate determination of the arrangement of the various structures occurring in this region of the body is rather difficult, but it seems fairly clear that that part of the œsophagus which is ventrally situated is continued backwards for a short distance and finally widens into the intestine, whilst from its dorsal side, in the vicinity of the nerve-ring, there arises a kind of tongue of glandular tissue which is continued posteriorly for a considerable distance. In the present species, as the figure shows, it reaches to a point a long way behind the muscular bulb. Its substance is finely granular and in one specimen there were indications that the organ was made up of at least three large cells similar to the arrangement described by Cobb (1915) in *Tylenchus similis* and by Stewart (1921) in *Aphelenchus ritzema-bosi*. By careful focusing two or three large nuclei could be seen lying within the protoplasm. It is to be regarded, no doubt, as a compound salivary gland homologous with the glandular posterior region of the œsophagus in the more typical members of the genus *Tylenchus*. In *A. tenuicaudatus*, de Man describes and figures a large glandular structure of undetermined character corresponding exactly in size and position with that in the species under description. He does not, however, show its anterior connection with the œsophagus.

It is necessary to deal with this region of the body at some length because it has rarely been clearly described even in recent accounts of *Aphelenchus* species. The arrangement of the structures described above, however, appears to be characteristic of the genus *Aphelenchus*. The writer has found it in the type species *A. avenæ* (see p. 212), in the very common free-living species *A. parietinus* and in all the plant-parasitic members of the genus which he has had an opportunity of examining: *A. olesistus* from ferns, *A. fragariæ* from strawberries, and *A. ribes* from black-currant buds. Stewart (1921) also described it in detail in *A. ritzema-bosi* from chrysanthemums and figured it in *A. olesistus* and *A. fragariæ*.

It will probably be readily understood from what has been said

concerning the ill-defined character of the immediately post-bulbar region of the œsophagus that it is very difficult to say where the œsophagus ends and where the intestine begins. All that can be said is that there is a gradual widening of the alimentary tract and an increase in the number



Aphelenchus winchesi n.sp.

Figs. 3 and 4.—Anterior end of male highly magnified showing arrangement of buccal stylet, œsophagus, nerve-ring and excretory pore and the disposition of the salivary glands. Fig. 4 is a continuation of Fig. 3.

Fig. 5.—Tail end of male showing spicule and caudal papillæ drawn to the same scale as Figs. 3 and 4.

of coarser granules in its walls, and one is probably justified in then speaking of this as the beginning of the intestine. The lumen, too

becomes wider and is continued posteriorly through the body to within a short distance of the anus with which it is connected by a short rectum. The excretory pore is situated, as in most of the other species of the genus, a short distance behind the level of the muscular bulb.

Female characters.—Principal measurements: Total length, 0.8 mm. to 0.93 mm.; greatest width, 0.025 mm. to 0.03 mm.; stylet, 0.024 mm. to 0.027 mm.; œsophagus, including bulb, from anterior end, 0.08 mm. to 0.09 mm.; anterior end to posterior limit of salivary gland, 0.2 mm. to 0.25 mm.; anterior end to vulva, 0.56 mm. to 0.67 mm.; anterior extent of gonad, 0.37 mm. to 0.47 mm.; anus to tip of tail, 0.12 mm. to 0.13 mm. Two immature females had total lengths of 0.6 mm. and 0.64 mm. respectively.

As the measurements show, the vulva is situated at about three-quarters of the body length from the anterior end. It leads by a short vagina into the uterus which, so far as can be determined from the few specimens available, is without a post-vulvar diverticulum such as occurs in many other species of the genus. In this respect it differs from *A. tenuicaudatus* which possesses a post-vulvar sac. The uterus is not very large and in the two mature worms examined contained one or two rather long eggs. Anteriorly it leads into a somewhat thickened and twisted part of the gonad tube, which is, perhaps, to be considered as a receptaculum seminis or merely as a posterior part of the oviduct. Spermatozoa have not definitely been seen within it. This region is succeeded by the ovary proper, which consists of a strand of cells progressively diminishing in size as one proceeds anteriorly. In the largest female found the anterior end reaches to about half the length of the salivary glands and is not bent back upon itself. In this it agrees with *A. tenuicaudatus*.

Male characters.—Principal measurements: Total length, 0.66 mm. to 0.68 mm.; greatest width, 0.022 mm. to 0.024 mm.; stylet, 0.024 mm. to 0.027 mm.; œsophagus, including bulb, from anterior end, 0.08 mm. to 0.084 mm.; anterior end to end of salivary gland, 0.17 mm. to 0.23 mm.; anus to tip of tail, 0.066 mm.; greatest length of dorsal part of spicule, 0.017 mm.

In the two males found the posterior end is curved towards the ventral surface. As fig. 5 shows, the body tapers gradually as far as a point a

little posterior to the level of the post-anal caudal papillæ, when it narrows rather suddenly by a rounded curve on the dorsal side and is continued into a finely tapering tail.

There is one pair of post-anal papillæ situated sub-ventrally some distance behind the anus. There are no pre-anal papillæ. The lips of the cloacal aperture are rather prominent and after very careful examination of this region the writer concludes that there is a pair of very indistinct ad-anal papillæ similarly situated to those figured and described by Micoletzky (1921), p. 595, in *A. parietinus*. They are very difficult to distinguish and are only seen on careful focusing under the oil-immersion.

There is a pair of spicules lying very close together. Each has a rose-thorn shape when viewed laterally as shown in fig. 5. The spicule is broadest at its base where its dorsal anterior end is produced into a rather long rounded prominence. Just within the cloacal aperture, in the lower wall, there is a rather hyaline structure which may perhaps be regarded as a weakly developed gubernaculum. It is very indefinite in outline. The gonad is single and extends anteriorly in the body to a point about midway of the length of the salivary glands. Its end is not reflexed and its structure calls for no special comment.

Discussion.—*A. winchesi* is very closely similar to *A. tenuicaudatus*, which it resembles in general shape in both sexes, in the shape of the female tail, in having a long stylet without basal swellings and in possessing long prominent salivary glands.

It differs from it in not having six distinct lips and in the female not having a post-vulvar uterine sac, though this difference is not emphasised as the writer's material is limited in amount and further examination of mature females might reveal its presence. The male of *A. winchesi* differs from that of *A. tenuicaudatus* in the greater length of its tail and in the number and disposition of the caudal papillæ. The differences are admittedly small, but are of such a character that the writer, after careful consideration, has come to the conclusion that it is advisable to create a new species for the reception of his organisms rather than cause confusion by assimilating them to de Man's *A. tenuicaudatus*.

Occurrence.—Extracted from pig-manure, July, 1927, Winches Farm, St. Albans, Herts.

Type material.—Six specimens, four females, two males, fixed in Ditlevsen's mixture and mounted in weak glycerine.

(2) *Aphelenchus avenæ* BASTIAN, 1865, TYPE SP., WITH A DISCUSSION
ON THE GENUS.

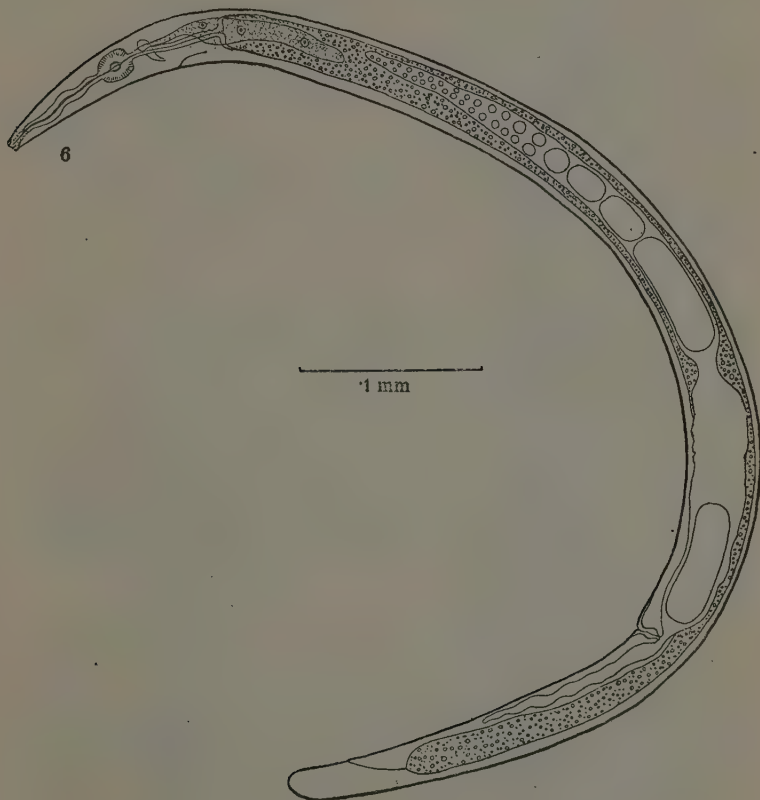
The type species of the genus is *A. avenæ* Bastian, 1865. It was not given this rank by Bastian in his original description, but we find it so designated by Stiles and Hassall (1905) in their "Determination of Generic Types." On p. 52 of this publication, under "Genera for which Types have been selected in Later Publications," we find it listed as follows: "*Aphelenchus* Bastian, 1865 (*avenæ* designated by Bastian), see p. 87" and on referring to this page we find the following: "*Aphelenchus* Bastian, 1865c, 93. 121-124. Type species designated by Bastian in letter to Stiles, dated March 22nd, 1904."

The worm is by no means of common occurrence, and it is to be regretted that it should have been designated as type of the genus 39 years after its original description, for in addition to its scarcity the species is only represented by females; males being quite unknown. The writer has encountered worms belonging to this species on three separate occasions: in rotting roots of a pea seedling in 1924, in a diseased potato tuber in autumn, 1926, and in decaying bulbs of *Narcissus moschatus* collected on the Spanish side of the Pyrenees and sent for examination in September, 1927. The opportunity has been taken of studying it in some detail, and it seems worth while to give an account of its structure.

The original description of *A. avenæ* given by Bastian (1865) is very brief, and his two figures, one of the head and the other of the tail, are not particularly good. He points out, however, that both ends of the body are rounded, and his figure shows a broad rounded tail. He also says that the dart—*i.e.*, the stylet—is simple and not knobbed at the base. Males were not seen and the species was obtained from between the lower sheaths of oats from a stubble field at Broadmoor, Berks.

Bütschli (1873) described and gave a good figure of the worm. de Man (1884), pp. 138-139, gave an account of *A. agricola*, which the drawings on Pl. 21, fig. 90, a-d, clearly show is the same as *A. avenæ*; the tail is rounded and the stylet is without swellings. He remarked on its close similarity to the latter species, but pointed out that he did not identify it with *A. avenæ* owing to its smaller size and different habitat.

Micoletzky (1921) recognises de Man's *A. agricola* as a synonym of *A. avenæ*.



Aphelenchus avenæ Bastian, 1865.

Fig. 6.—Low-power drawing to show the principal anatomical features.

Morphology.

Principal measurements:—Total length, 0·8 mm. to 0·95 mm.; greatest width, 0·28 mm. to 0·33 mm.; stylet, 0·018 mm. to 0·02 mm.;

oesophagus, including bulb, from anterior end, 0·08 mm. to 0·11 mm. ; anterior end to vulva, 0·6 mm. to 0·65 mm. ; anus to tip of tail, 0·03 mm. to 0·034 mm. ; anterior extent of gonad, 0·47 mm. to 0·5 mm.

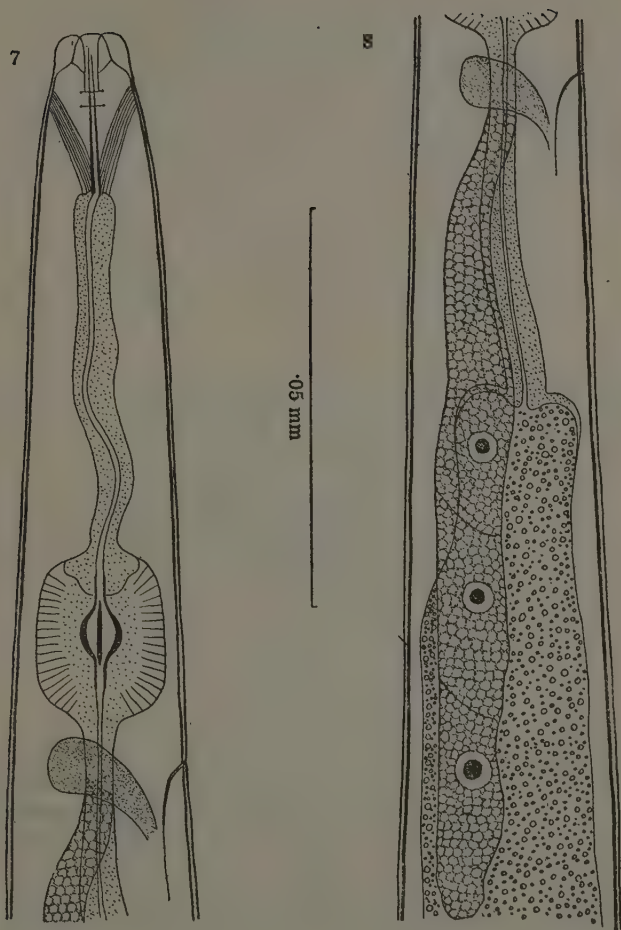
Fig. 6 shows the chief anatomical features of the worm and a long description is unnecessary.

The head end is narrower than the tail, which is blunt and rounded. Examination under high powers shows that there is a distinct lip region set off by a shallow groove from the rest of the body. In optical section the edges appear rounded, and by careful focusing on the surface the lips appear to be completely fused together, so that there are six facets separated by slight ridges. Behind this region the cuticle of the body is transversely striated.

The mouth is anterior and central and leads into a short vestibulum about one-sixth the width of the lip region. The stylet has a length of from 0·01 mm. to 0·02 mm. and has no basal swellings. The aperture lies just behind the point on the ventral side. There are two transverse guides, one at the base of the vestibulum and the other slightly more posterior in position. The lumen of the stylet leads into that of the oesophagus, the first part of which has a width of about one-third of the body in the region where it lies. It narrows a little before expanding into the large muscular bulb, at the centre of which are found the three crescentic expansions of the cuticular lining which serve for the attachments of the muscles.

Posterior to the bulb the oesophagus is continued for a short distance at about the same width as the oesophagus just anterior to it. Here the nerve-ring crosses it and the excretory pore is to be seen on the ventral surface in close proximity. The oesophagus extends backwards from the bulb to a distance almost as great as the length of the pre-bulbar portion and has a width practically the same as the latter. It then swells out into the intestine with cellular walls containing granules and oil globules.

As in *A. winchesi*, just posterior to the bulb the salivary glands are given off on the dorsal side of the oesophagus and stretch backwards in a dorso-lateral position over the anterior end of the intestine, appearing as a distinct lighter lobe of finely granular material. Faint outlines of the three large cells composing the glands were distinguishable. This arrangement of parts has been determined by careful examination under the oil-



Aphelenchus avenae Bastian, 1865.

Figs. 7 and 8.—Anterior end highly magnified to show arrangement of the buccal stylet, oesophagus, nerve-ring, excretory pore and the disposition of the salivary glands. Fig. 8 is a continuation of Fig. 7.

immersion of worms viewed in lateral, ventral and dorsal aspects. The intestine and rectum call for no special description.

The vulva is situated at a point slightly more than three-quarters of the body length from the anterior end. It is connected by a short vagina with the uterus which has a well-marked post-vulvar diverticulum. Anteriorly the uterus is continued for a short distance as a fairly wide tube and occasionally one or two eggs may be seen within it. Towards its forward end the wall is seen to be distinctly cellular and one gets the impression that spermatozoa are located in this region. If this is so the worms are probably not parthenogenetic, but syngonic protandrous hermaphrodites, *i.e.*, both kinds of sex-cells are produced from the one gonad. Such species are already known amongst the free-living nematodes.

The ovary is separated from the uterus by a slight constriction and gradually decreases in width as it extends anteriorly. It may reach as far as the posterior end of the salivary glands, but in some specimens does not. It does not appear to be reflexed upon itself.

As already pointed out, *A. avenæ* is represented only by females; it becomes necessary, therefore, to establish what male characters shall be considered as typical of the genus *Aphelenchus*. In the writer's opinion this can best be done by taking those of *A. parietinus*, a well-known and widely distributed species. In doing this one is actually following the example of Micoletzky (1921), who has selected *A. parietinus* as the basis of his account of *Aphelenchus* in the true sense.

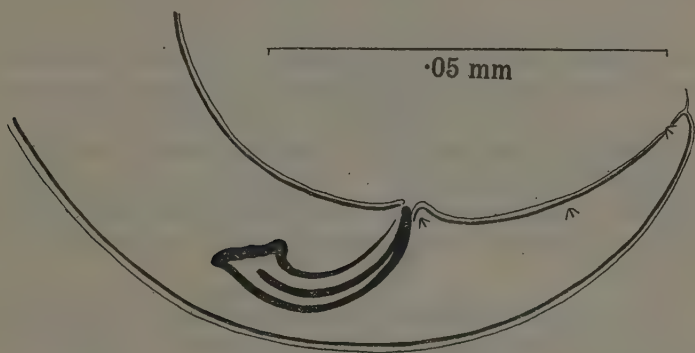
The species differs from *A. avenæ* in a few features; the head is distinctly knobbed, the stylet has three basal swellings and the tail in both sexes is provided with a small terminal process. The post-bulbar arrangement of the œsophagus and salivary glands is on the same lines, however, as in *A. avenæ*, and the species is clearly to be considered as belonging to the genus *Aphelenchus*.

The male tail is, as a rule, ventrally bent and is without lateral alæ. According to de Man (1876), Cobb (1918) and Micoletzky (1921) there are three pairs of caudal papillæ; one pair ad-anal or immediately post-anal, another pair situated about midway between the cloacal aperture and the tip of the tail, and a third pair almost terminal in position. All three pairs are sub-ventrally situated. The spicules are closely applied to each

other laterally, and each is shaped rather like a thorn when seen in side view with the point towards the cloacal aperture. The base of each is almost straight and the body of the spicule appears to be hollow.

Having now obtained an idea of the chief morphological features of the type species and the male characters of a closely allied species, we may perhaps attempt to define the generic characteristics of *Aphelenchus*.

Small worms tapering anteriorly and posteriorly; head end knobbed or only slightly set off from the body; lips more or less distinct, generally



Aphelenchus parietinus Bastian, 1865.

Fig. 9.—Tail end of male highly magnified showing spicule and caudal papillæ.

not; tail blunt and rounded or tapering to a point, with or without terminal process. Buccal stylet long or short, with or without basal swellings. Œsophagus made up of a pre-bulbar narrow portion, a distinct muscular bulb with conspicuous crescentic expansions of the lumen at the centre, a short and more or less distinct post-bulbar portion merging gradually into the intestine. Arising from the Œsophagus very soon after the bulb in a dorso-lateral position, the salivary glands extend posteriorly over the anterior end of the intestine and appear as a lighter lobe.

Vulva at the beginning of the posterior third or quarter of the body, uterus generally with and rarely without a post-vulvar diverticulum, gonad single and outstretched anteriorly with terminus of ovary straight or reflexed.

Male tail usually curved ventrally, without caudal alæ. Caudal papillæ up to three pairs, ventro-lateral and mostly post-anal in position. Spicules very closely applied to each other and each shaped like a rose-thorn when viewed laterally with the point directed to the cloacal aperture. Gubernaculum absent or rudimentary.

DISCUSSION.

Aphelenchus avenæ and its near relatives.

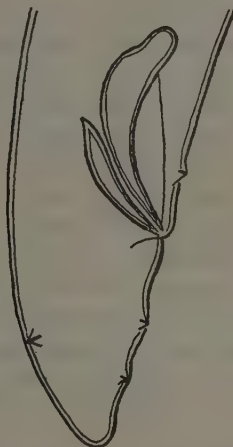
From the description of the arrangement of the post-bulbar part of the œsophagus and the salivary glands already given it will be gathered that the writer considers this as characteristic of the genus *Aphelenchus*. The structures and their lines of separation are frequently very difficult to distinguish, but it is quite clear that there is generally no well-defined post-bulbar œsophagus such as is found in many species of the genus *Tylenchus*. This being so it is of interest to consider certain forms closely allied to *Aphelenchus* in which a definite post-bulbar œsophagus has been described.

Micoletzky (1921), pp. 602-605, describes and figures a species closely related to *A. avenæ* under the name of *Aphelenchus* (*Paraphelenchus*) *pseudoparietinus*, giving the worms sub-generic rank. Females only were found by him and they are shown as having a distinct œsophagus behind the muscular bulb traversed by a narrow lumen leading into the granular intestine. In the character of the head and tail the worms are very similar to *A. parietinus*, the head being knobbed and the tail having a short terminal process.

de Man (1921), pp. 39-40, gives an account of two male worms which he considers to be the males of his *A. agricola*. He deals at length with the post-bulbar region of the œsophagus, and his fig. 27 clearly shows a definite œsophagus here, almost as long as the pre-bulbar region, traversed by a narrow lumen. It seems clear to the writer in comparing de Man's figure and description with that of Micoletzky that he was dealing with males of the same species as Micoletzky's organism or with a very nearly related species and not with the males of *A. avenæ*. It is by no means clear in the case of both de Man's and

Micoletzky's accounts where the salivary glands are or how they are disposed.

There are certain important features in the male tail described by de Man which clearly indicate that the worms do not belong to the genus *Aphelenchus*. There are apparently four pairs of caudal papillæ, one



Aphelenchus agricola de Man, 1921.

Fig. 10.—Tail end of male $\times 1200$, showing spicule, gubernaculum and caudal papillæ (After de Man). It is regarded by the writer as a species of *Paraphelenchus* Micoletzky.

ventral and pre-anal, two ventral and post-anal and one dorsal and post-anal. The spicule has an altogether different shape from the thorn-like spicule of the true *Aphelenchi* and in addition there is a large gubernaculum. Each spicule is slightly swollen anteriorly, with a small constriction between the rounded end and the main portion. Reference to fig. 10, which is a copy of de Man's figure, will render the differences more apparent than any description.

A recent paper by Steiner (1926) furnishes additional evidence of the difference of *A. (Paraphelenchus) pseudoparietinus* from true species

of *Aphelenchus*. Amongst certain nematodes found by him in diseased pea-nuts sent from South Africa there were a few examples which Steiner identified as *A. (Paraphelenchus) pseudoparietinus*, and representatives of both sexes were found. The description and drawing of the male tail show that the worm possesses spicules very similar in appearance to those figured by de Man with anterior knob followed by a slight constriction. The gubernaculum is spoken of as small and this is a point of difference from de Man's worm which is shown as having a comparatively large gubernaculum. There are also two ventro-median caudal papillæ and probably another pair in the vicinity of the anus, though this is uncertain. Comparison of de Man's and Steiner's figures leaves no doubt in the writer's mind as to the very close kinship and probable identity of the worms found by these investigators. It is also clear that de Man's so-called males of *Aphelenchus agricola* are not really members of the genus *Aphelenchus* but should be placed in Micoletzky's *Paraphelenchus*. The latter, by reason of the well-defined post-bulbar œsophagus and the character of the spicules, gubernaculum and the male caudal papillæ, should be taken from the position of a sub-genus and given generic rank. The writer, herewith, raises *Paraphelenchus* sub. gen. Micoletzky 1921, to *Paraphelenchus* gen. nov.

The present discussion affords a suitable opportunity for drawing attention to the close similarity between the anterior end of *A. avenæ* and that of *Isonchus radicolus* Cobb 1913. The latter is very briefly described by Cobb and his figure merely shows the extreme anterior end having a stylet without basal swellings. In another paper—Cobb (1914)—there is on p. 478, fig. 39, a drawing of a considerable portion of the anterior end of a worm which Dr. Cobb informed the writer by letter was made from *Isonchus radicolus*. The lip region, the simple stylet, the first part of the œsophagus, the muscular bulb and the situation of the nerve-ring and excretory pore are all practically identical with these structures in *A. avenæ*. It would be of great interest to have further information on the arrangement of the œsophagus and salivary glands in the post-bulbar region of *Isonchus*. At present all the original account tells us is that the posterior swelling is fully half as wide as the neck and ends indefinitely.

The male tail is figured in the 1913 paper and it is to be noted that the spicules as drawn there bear a strong resemblance to those given by de Man (1921) for his *A. agricola*. The great difference presented by *Isonchus*, however, is that it has caudal alæ forming a kind of bursa with supporting papillæ. Unfortunately the female tail is not drawn nor is its shape described.

In the writer's opinion the genus *Isonchus* is very closely related to *Paraphelenchus* and further investigation of these two genera is much needed so that their relationship to each other and to the genera *Aphelenchus* and *Tylenchus* may be better understood.

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CORRIGENDA FOR VOLUME V.

- Page 1, eighth line from bottom, for "species" read "genera."
- Page 3, end of first line, after "table" add "is."
- Page 4, line 4, for "*Prostrongylus*" read "*Protostrongylus*."
- Page 6, line 23, for "arises" read "arise."
- Page 6, line 24, for "are" read "is."
- Page 6, at beginning of last line, add "or by the deposition."
- Page 11, fourth last line, for "entire" read "étirée."
- Page 16, second last line, for "Fron" read "From."
- Page 21, second line, for "*mustelorum*" read "*mustelarum*."
- Page 22, third last line, for "with the rectum" read "with the intestine."
- Pages 1-24, throughout this article for "telemon" read "telamon."
- Page 166, fifth last line, for "irregula" read "irregular."

